Comparative study of episodic memory in common cuttlefish (Sepia officinalis) and Eurasian jay (Garrulus glandarius)

Pauline Billard

Normandie Université

THÈSE

Pour obtenir le diplôme de doctorat

Spécialité SCIENCES DE LA VIE ET DE LA SANTE

Préparée au sein de l'Université de Caen Normandie

Etude comparative de la mémoire épisodique chez la seiche commune (Sepia officinalis) et le geais des chênes (Garrulus glandarius)

Présentée et soutenue par
Pauline BILLARD

Thèse soutenue publiquement le 18/12/2020 devant le jury composé de		
M. MATHIAS OSVATH	Professeur, Université de Lund - Suède	Rapporteur du jury
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Ethologie Animale et Humaine
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THESE

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Spécialité Physiologie et Biologie des Organismes – Populations - Interactions

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SUMMARY TABLE

Publications

Included in this thesis:

Chapter 1:

Billard, P., Clayton, N. S., Jozet-Alves, C. (2019). Episodic Memory. In Jennifer Vonk and Todd K. Shackelford (dir.). Encyclopedia of Animal Cognition and Behavior. Springer.

Chapter 2:

Billard, P., Clayton, N. S., Jozet-Alves, C. (2020a). Cuttlefish retrieve whether they smelt or saw a previously encountered item. Scientific Reports, 10:5413. DOI: 10.1038/s41598-020-62335-x.

Billard, P., Jozet-Alves, C., Clayton, N. S. (in revision in Animal Behaviour and Cognition). A new paradigm for assessing discriminative learning and incidental encoding of task-irrelevant contextual cue in Eurasian jay.

Chapter 3:

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Billard, P., Coll, S. Y., Glowinski, D., & Grandjean, D. (2020). Language is the missing link in action-perception coupling: an EEG study. Scientific Reports, 10(1):14587. DOI: 10.1038/s41598-020-71575-w.

ABBREVIATIONS/ACRONYMS

BA	Anterior basal lobe
BP	Posterior basal lobe
Br	Brachial lobe
C	Cortex
ELM	Episodic-like memory
FI	Inferior frontal lobe
LTM	Long-term memory
MTT	Mental time travel
N	Neuropil
Olf O	Olfactory organ
Pal	Palliovisceral lobe
Ped	Pedal lobe
PPE	Postpartum oestrus
Pr	Precommissural lobe
SF/FS	Superior frontal lobe
SF LC	Left superior frontal lobe cortex
SF LN	Left superior frontal lobe neuropil
SF RC	Right superior frontal lobe cortex
SF RN	Right superior frontal lobe neuropil
SMF	Source-monitoring framework
SV	Subvertical lobe
SV LN	Left subvertical lobe neuropil
SV RN	Right subvertical lobe neuropil
SV LC	Left subvertical lobe cortex
SV RC	Right subvertical lobe cortex
VL/V	Vertical lobe
VL LC	Left vertical lobe cortex
VL LN	Left vertical lobe neuropil
VL RC	Right vertical lobe cortex
VL RN	Right vertical lobe neuropil

List of Figures

1. General introduction

As far as we experience it, time is linear, moving forward from the past to the future. Despite the amazing inventions imagined by sci-fi authors (e.g., *The Time Machine*, Wells, 1985), it is literally impossible to travel physically into the past or the future. However, every day we modify our past and our future even without being aware that we are doing so. Indeed, we can travel through time *mentally*. This capacity to project into the past and the future mentally is called mental time travel (MTT), and is presented as a very defining capacity of human beings.

MTT can be divided in two components: a retrospective component (travelling into the past) and a prospective component (travelling into the future). The retrospective component is known as episodic memory. It was originally defined by Tulving in 1972, and its definition has evolved until recently (Tulving, 2005). In the latest definition of episodic memory, Tulving distinguished between the content of episodic memory and its phenomenology making this type of memory unique among the other memory types. The content of episodic memories involves spatio-temporal information allowing individuals to retrieve where and when the memory was formed. The phenomenological sides of episodic memory include the awareness of time (i.e., I know that I am living in the present, that my memories are in the past, and that tomorrow is the future), and of oneself (I know that my memories belong to my personal past and not from someone else). The prospective component of MTT is called episodic future planning (or also episodic future thinking, Atance & O'Neill, 2001). While they were thought as being completely independent, the retrospective and the prospective components of MTT are now considered as answering the same goal. The capacity to remember the past (i.e., episodic memory) would serve future purposes by allowing to anticipate and plan future events (e.g., Schacter and Addis, 2007; Schacter & Madore, 2016).

From humans…

The capacity to travel mentally through time is omnipresent in our daily-life. Early in the development, children are asked to project themselves into the past or the future. For instance, they are often asked to imagine what they would like to become as adults, what they would like to do next weekend, or what they did during the day at school (Martin-Ordas, 2016). It was shown that adults talk about past and future events in more than half of their conversations (Szagun, 1978). Our societies value individuals who have the capacity to anticipate the future, a capacity involved in most of our everyday activities: For instance, planning the different tasks that need to be done as part of a business project, or when simply playing chess.

MTT allows us to reconstruct past episodes, evaluate present situations, and anticipate the future. It has been argued that episodic memory is crucial for social interactions in humans because they need to remember the past actions of another individual to interact adaptively with them (e., Klein et al., 2009). An impaired MTT capacity entails human's capacity to understand their world and other individuals (e.g., amnesic patients who cannot remember their past and don't recognize their relatives). Neuropsychological studies on these patients led authors to assume that humans' ability to remember and project into their future seems necessary to build their identity (e.g., Lin, 2020; McCarroll and Cosentino, 2020). Thus, when MTT abilities are impaired, such as in amnesia for instance, the feeling of self and identity are impacted (see for instance Corkin, 2002 or Klein and Nichols, 2012).

…To other animals

To survive in the wild, animals learn and memorize from their experiences. For instance, young cats learn how to catch a mouse without making noise, climb trees, groom themselves and so on. This capacity to learn and memorize things is crucial for animals to stay optimally adapted to their environment, and there is a broad consensus in the scientific literature that all animals possess this ability (e.g., Kamil and Roitblat, 1985; Healy and Jones, 2002). What is more debated, is animal's understanding of time, and whether they can project mentally into the past or the future. In other words, whether they possess episodic capacities.

Possessing episodic abilities can also be adaptive for non-human animal species. Animals need to forage for food in various environments and the capacity to remember which prey or food was encountered and in which context (i.e., time and place) may be crucial. For animals caching food, the capacity to remember when the cache was made allows to recover the perishable food before it is not edible anymore. Animals also need to remember the occurrence of other's behaviour (e.g., this young male fought with an older male and won the fight) and replace it in time to display appropriate social behaviour (e.g., the young male is now higher in the hierarchy and the other individuals need to show subordinate behaviours in front of him, while this older man was the previous dominant).

Over the past 30 years, researchers have documented on animal capacity to remember personal events or anticipate the future. Even though the opinions of researchers stating that MTT is unique to humans has evolved, the debate focussing on whether animals are able to mentally travel through time is still on. This is due in part to the difficulty to investigate episodic cognition through non-verbal tasks in animals and to interpret animal's behaviour in these tasks.

To enrich the debate, it seems now necessary to create new non-verbal behavioural to investigate a wider range of species and a wider range of episodic cognition features. Investigating the differences and similarities of different aspects of MTT abilities in evolutionary distant species can help our understanding of how these complex cognitive capacities have evolved under different environmental constraints.

2. Objectives of this PhD thesis

The primary goal of my PhD thesis project is to provide new empirical data on mental time travel in animals. This work is developed in a comparative perspective to investigate different aspects of mental time travel in a cephalopod mollusc, the common cuttlefish (*Sepia officinalis*) and in a bird species, the Eurasian jay (*Garrulus glandarius*).

The common cuttlefish is part of invertebrate family which have been understudied in the complex cognition literature, and only one study has investigated its capacity to manipulate episodic information (i.e., the what-where-when content of episodic memories, Jozet-Alves et al., 2013). To counterbalance this lack of data, it seems important to test whether such cuttlefish cognitive abilities fulfil the other episodic-like memory criteria, such as flexibility. As episodic memory has been recently described as a way to plan for the future (e.g., Schacter and Madore, 2016), this PhD thesis will also investigate cuttlefish capacity to act in the present according to future environmental conditions (future-oriented behaviour) and according to future needs (future-planning).

This PhD work aims at exploring a new way to investigate episodic-like memory in animals: source-memory. Source-memory is the capacity to retrieve specific features composing the initial event to remember its source (e.g., who told me the information, did I hear it on the radio or did I see in on the news, etc; Johnson et al., 1993). The results obtained from two different source-memory experiments will be compared in cuttlefish and jays. Contrary to the cuttlefish, a large number of studies were conducted on jay's capacity to remember the content of episodic memories (e.g., Clayton and Dickinson, 1998), to use this content flexibly (e.g., Clayton et al., 2003b), and to plan for the future (e.g., Raby et al., 2007). The source-memory experiment in jays will investigate an aspect that has not been investigated yet while being a crucial defining feature of episodic memory, namely jay's capacity to incidentally encode information. This aspect will bring innovative data the already existing scientific literature about episodic cognition in jays.

Cuttlefish and jays are two different species which evolved differently from the vertebrate lineage around 500 million and 300 million years ago. Studying source-memory in a comparative manner can shed light on its differences and similitudes in cuttlefish and in jays and help understand how it has evolved under different environmental constraints.

3. Manuscript organization

Four chapters compose this PhD thesis:

Chapter 1 (LITERATURE BACKGROUND AND MODEL PRESENTATION) of this thesis presents a review of the literature on mental time travel in animals. It includes a first section on **episodic cognition** comprising a subsection on *episodic memory* in humans and on *episodic-like memory* in a wide range of species, from vertebrates to invertebrates. Another subsection focuses on *source-memory* as it is described in humans and how it has been studied in animals. Next, in a second section named **comparative study of cognition**, I will first present a short overview of the history of the field of *comparative cognition*, to better appreciate the scientific framework of my project. Then, I will conclude this section with the description of the two *animal species studied* during my PhD thesis: the common cuttlefish and the Eurasian jay.

Chapter 2 (EXPLORATION OF SOURCE-MEMORY IN CUTTLEFISH AND JAYS) focuses on source-memory. It provides new data on *source-memory in cuttlefish* using a source-discrimination task, inspired from human's studies of source-memory. It also presents a new way to investigate *source-memory in jays* using an incidental encoding paradigm.

Chapter 3 (EXPLORATION OF FUTURE PLANNING) presents two studies of *future-oriented behaviour* in cuttlefish. Specifically, one study focuses on cuttlefish ability to flexibly adapt their predatory behaviour in the present according to their past experience and to predictable future events. The other study investigates whether cuttlefish could anticipate their future needs independently of their current needs.

Chapter 4 (NEURONAL SUBSTRATES OF EPISODIC-LIKE MEMORY IN CUTTLEFISH) presents an investigation of the *neuronal substrates of episodic-like memory* in cuttlefish brain.

Finally, all the results obtained during the behavioural and neurobiological experiments mentioned before are discussed in the **General discussion**.

Articles published in international reviews are inserted in the manuscript. To facilitate its lecture, the page numbering of the inserted articles as well as the headings of the figures have been updated to follow the present organization of the manuscript. Every chapter is followed by a summary outline.

CHAPTER

1

LITERATURE BACKGROUND AND MODEL PRESENTATION

Book chapter 1:
Billard, P., Clayton, N. S., Jozet-Alves, C. (2019). Episodic Memory. In Jennifer Vonk and Todd K. Shackelford (dir.), Encyclopedia of Animal Cognition and Behavior. Springer.

Introduction of Chapter 1

This introductory chapter aims at presenting the literature background of this PhD thesis. First, I will give an overview of episodic memory and source memory, two aspects of mental time travel that I have focussed on during my PhD. Then, I will introduce the past and current place of comparative cognition in the scientific field of animal cognition leading me to present the two very different animal species studied in this thesis.

Section A: Episodic cognition

I. Episodic memory: In this subsection, a definition of episodic memory is given, with its issue in terms of human uniqueness. Then, we will see why authors prefer to employ the expression episodic-like memory in animals instead of episodic memory and how it is tested in different species. Other aspects of episodic cognition are briefly discussed in this part: source-memory and future-oriented behaviour.

II. Source-memory: Here, we will define source-memory in more details, including the way it is tested in humans and in animals.

Section B: Comparative study of episodic cognition

I. Comparative cognition: In this subsection, we will discuss the way the comparative cognition field has emerged and how researchers study animal cognition in a comparative perspective. Questions such as "Does it make sense to investigate only one animal after the other, or would it be better to study several species with the same question?" will be **approached.**

II. Presentation of the species studied: In this subsection, I will present the two animal species studied in this PhD thesis. Understanding how both species live, perceive their environment, and forage for food is crucial to design appropriate cognitive tests.

A. Episodic cognition

I. Episodic Memory

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Abstract

Episodic memory is the capacity to retrieve spatially and temporally dated personal past events. Defined as being essentially a human's characteristic, researchers questioned the unicity of episodic cognition in the study of animal's ability to project into the past and the future. To do so, they agreed on several behavioural criteria of episodic-like memory, allowing to study animal's capacities to retrieve *what* was encountered, *when* and *where* it was encountered. The following chapter reviews the different studies investigating this episodic-like memory in various animal's species, and presents other ways to study episodic cognition in animals such as source-memory and future-oriented behaviour.

Billard, P., Clayton, N. S., Jozet-Alves, C. (2019). Episodic Memory. In Jennifer Vonk and Todd K. Shackelford (dir.). Encyclopedia of Animal Cognition and Behavior. Springer.

Introduction

From antiquity, memory has fascinated intellectuals such as philosophers, artists, mathematicians, and more recently psychologists and neuroscientists. The definition of memory itself has evolved through time. The twentieth century has specifically impacted the study of memory. Under the influence of eminent scientists such as Bartlett (1886–1969), memory was no longer considered as a passive trace in the brain, but instead as an active process involving the reconstruction of previously encoded features. Human memory was divided into sensory memory (very short term memory receiving perceptual and sensitive information from environment), short-term memory (temporary storage of information), and long term memory (long-term storage of information, Figure 1). It is only during the second part of the twentieth century that long-term memory was divided in several types based on its different functions.

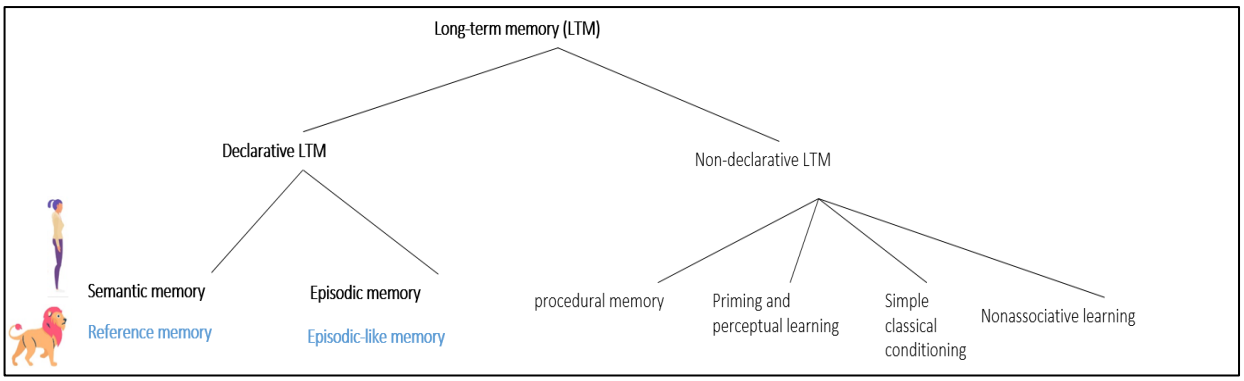

Figure 1 Taxonomy of long-term memory adapted from Squire (2004). This figure was added to the originally published book chapter.

Two broad long-term memory systems differing according to their accessibility to conscious recall (i.e., the capacity to retrieve information previously encoded) were described: the non-declarative and the declarative systems. Non-declarative memories, also called implicit or procedural memories (e.g., memory of habits, skills...), are characterized by an unconscious processing of information (e.g., cycling does not need a conscious access of previously learned motor memories). On the contrary, declarative memories (or explicit memory) are characterized by the conscious recollection of facts and events. These declarative memories are in turn divided into two forms, semantic knowledge or labels about the world (e.g., Paris is the capital of France) and episodic memories or experiences (e.g., what I wore and how I felt last time I went to Paris), a distinction first made by Tulving (1972, 1983). Episodic memory is the capacity to travel mentally back in one's personal past. Both episodic and semantic memories imply bringing memories into conscious awareness; however, consensus in the scientific community states that they differ in terms of the nature of information they convey (Tulving

Billard, P., Clayton, N. S., Jozet-Alves, C. (2019). Episodic Memory. In Jennifer Vonk and Todd K. Shackelford (dir.). Encyclopedia of Animal Cognition and Behavior. Springer.

1972, 1983). Semantic memory refers to general knowledge of the world (e.g., Paris is the capital of France), while episodic memory refers to the memory of personally experienced past events (e.g., a memory of a poignant moment spent with friends). Episodic memory involves contextual information pertaining to the previously experienced event (i.e., temporal and spatial information). The phenomenological aspects of episodic memory have been defined by Tulving (1972, 1983): namely, the personal and conscious recollection of an event that occurred in the personal past (i.e., I am aware that I am remembering a specific event from my past, and I know that I live in the present and that I can recall memories from my past or anticipate future events). One crucial phenomenological element is called autonoetic consciousness (i.e., self-knowing) and another is chronesthesia (an awareness of the passage of time). Together they build personal identity by accessing autobiographical information about how the self-moves and changes through time while maintaining identity and integrity (e.g., I am different from someone else, and my memories belong to my personal past). These phenomenological elements make episodic memory a very special type of memory precisely because it is rooted in self (i.e., one's identity), in time (i.e., the past), and in consciousness (i.e., being aware of the external environment and of one's internal state and how these make and maintain changes in the self through time). This definition of episodic memory in terms of consciousness has long led authors' claim that episodic memory is unique to humans. The distinction between episodic and semantic memory arose from neuropsychological studies of amnesic patients presenting an impairment of episodic recall while semantic knowledge was preserved. In these studies, patients were not able to create new episodic memories and to retrieve episodic memories from several years before their brain damage. That is, the owner of a semantic memory will know one fact he encoded in his semantic memory but will not be able to recall any contextual information present at the moment of encoding (e.g., temporal or spatial information). At the opposite, the owner of an episodic memory will remember this memory by recollecting the specific features present when the memory was formed (e.g., perceptual, sensitive, emotional, cognitive information). From a methodological point of view, episodic memories are created after a single presentation of an event. Multiple presentations of such an event would lead to semantic information processing. The crucial notion hidden behind these statements is the "expectation of being asked." Indeed, it is now debated whether animals should be asked unexpected questions in order to eliminate rule-based (i.e., semantic) explanation of the behavior to investigate episodic cognition in animals. Episodic and semantic memories would represent two parallel subsystems where episodic memory is embedded within semantic memory. According to Tulving (1983, p. 66), the two systems "can operate independently of

Billard, P., Clayton, N. S., Jozet-Alves, C. (2019). Episodic Memory. In Jennifer Vonk and Todd K. Shackelford (dir.). Encyclopedia of Animal Cognition and Behavior. Springer.

the other, although not necessarily as efficiently as it could with the support of the other intact system." The two systems seem to share cerebral structures, such as the hippocampus (Suzuki and Clayton 2000). That is, even if their functioning is different, episodic and semantic subsystems interact and are part of the same memory organization (Figure 2). Some researchers argue that remembering the temporal component of an episodic memory may involve retrieving contextual information instead of a specific timing, for instance, recalling which objects were present when the memory was encoded (Eacott and Norman 2004). The specific type of memory in charge of recalling contextual features that were present when the episodic memory was formed is called source-memory (Johnson et al. 1993). Episodic recollection is being triggered by contextual information; source-memory tasks are designed to study episodic memory. Episodic memory is the retrospective part of mental time travel which corresponds to the ability of re-experiencing of personal past event (remembering the past), and episodic future thinking is the pre-experiencing of future events (imagining the future) which involves the prospective nature of mental time travel. In this entry, we will assess the evidence for such systems in animals. Asking whether animals possess such episodic capacities for both the past and the future would help understand the function of the episodic cognition in an evolutionary perspective.

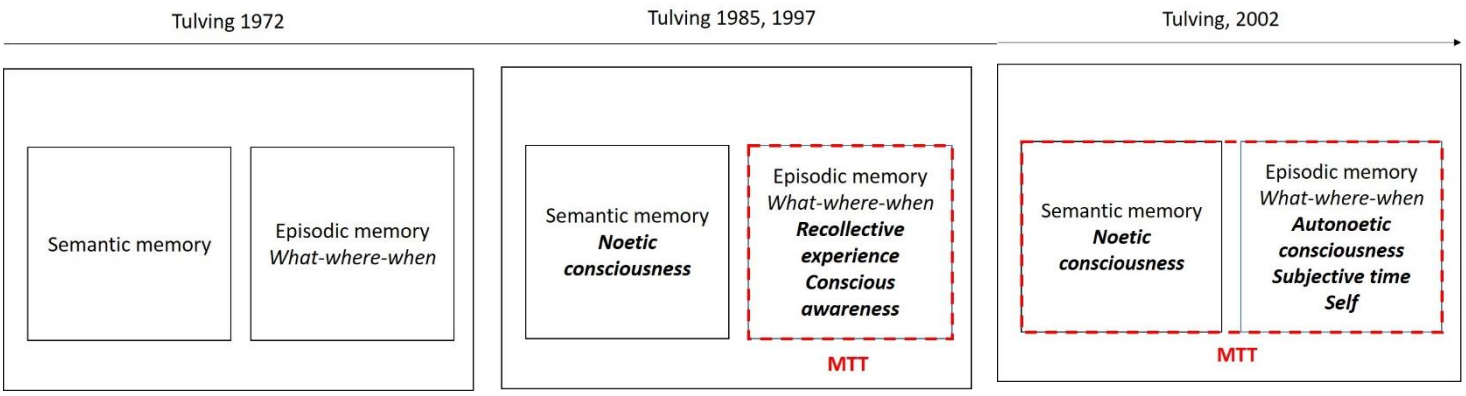

Figure 2 Evolution of the definition of episodic memory by Tulving from its conception in 1972. This figure was added to the originally published book chapter.

1. Episodic-Like Memory in Animals

There is an important debate as to whether mental time travel is unique to humans or shared with other animals. Bischof-Köhler (1985) claimed, for instance, that it is impossible for animals to anticipate future states because they are bounded into a present defined by their current motivational state, and Tulving (1983) suggested that animals do not remember personal past experiences. The "mental time travel" hypothesis stated also that the ability to mentally re-

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experience or pre-experience one's personal event is uniquely human (Suddendorf and Corballis 1997). Even though the debate is still vivid today, opinions have evolved since 1997 (e.g., Corballis 2013), in particular through research showing sequential replay in the rat hippocampus suggesting anticipation of future paths in a maze, as they either correspond to path rats have not actually taken or path rats previously took but in a temporally reversed order (Gupta et al. 2010). It led the author to admit that the difference between human and other animal's mental time travel ability might be one of degree and not of kind. One issue is the definition of episodic memory in terms of consciousness, i.e., of autonoesis and chronesthesia mentioned above. Phenomenological aspects of episodic memory are usually investigated through verbal tasks in humans. A classical approach is to ask whether adult humans are able to verbally express what they recall in opposition to what they know during an interview, giving details of when and where they learnt the information. As these tests are highly dependent on verbal abilities, they are not relevant for infants and toddlers, as well as animals. As no conclusive experiments have been developed to study the phenomenological aspects of episodic recollection in the absence of agreed non-linguistic criteria, it remains impossible to ask these individuals, be they nonverbal animals or preverbal children, whether they know or remember something. The study of episodic cognition in animals needs to rely on behavioral measures that can be objectively tested. Clayton et al. (2003a) suggested three main behavioral criteria to investigate episodic memory in animals, namely, the content (i.e., "what" happened, "when," and "where"), structure (i.e., the three features are bound together and integrated into one and the same episode), and flexibility (i.e., cardinal features of a declarative as opposed to a procedural system) of the memory. This minimalist view, circumventing the phenomenological aspects of episodic memory, refers to "episodic-like" memory. The content behavioral criterion of episodic like memory is based on Tulving's original definition (i.e., "a system that receives and stores information about temporally dated episodes or events, and temporal-spatial relations among these events" Tulving 1972). This definition means that an episodic memory provides information about "what" happened as well as "when" and "where" it happened. According to the authors, the "when" component is crucial as episodic memory is temporally unique, whereas the spatial component (where) and the event itself (what) can be shared by several episodic memories. The structure behavioral criterion of episodic-like memory implies that the content must represent an integrated representation of the three components acquired through a unique encoding. In other words, the "what," "when," and "where" must represent the same episodic memory. The flexibility behavioral criterion of episodic-like memory states that this integrated representation should be reused flexibly when required. Indeed, episodic memory is a subpart

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of the declarative memory system which supports the flexible deployment of encoded information. The description of these three behavioral criteria has allowed researchers to start investigating, at least from a behavioral point of view, whether or not this cognitive ability would possibly be present in nonhuman species. A wide range of species has been studied during the past decades using this theoretical background; it is noteworthy that researchers were differently assessing the temporal component of episodic like memory. In the following sections, we will review some of the studies using different definitions of this component.

2. Studies Using the What-Where-When Criterion

Time can be defined as a continued and linear movement occurring irreversibly from the past through the present to the future. One single exception is the capacity of mental time travel allowing one to look back into the past and look forward into the future. Episodic memory is thus deeply rooted in temporality. Measuring this temporality can be done in several ways. Friedman (1993) discusses three main different theories to consider time. The first focuses on the event's distance from the present. The remembered event is dated based on the time expired from the actual present (distance-based theory: i.e., how long time ago). The second approach assumes that the event itself shares information about the age of the memory (location-based theory or absolute timing theory: e.g., date of the calendar). The last approach is based on the relative time of occurrence of the memory where the date of the memory is determined according to other events (order-based theory: i.e., event B occurred after event A and before event C). In this conception, the date of the memory is determined in relation with other events (before/after judgments).

Time is a process of active, repeated construction. In the following section, we will give some behavioral examples of experiments using these different approaches to investigate episodic-like cognition in animals.

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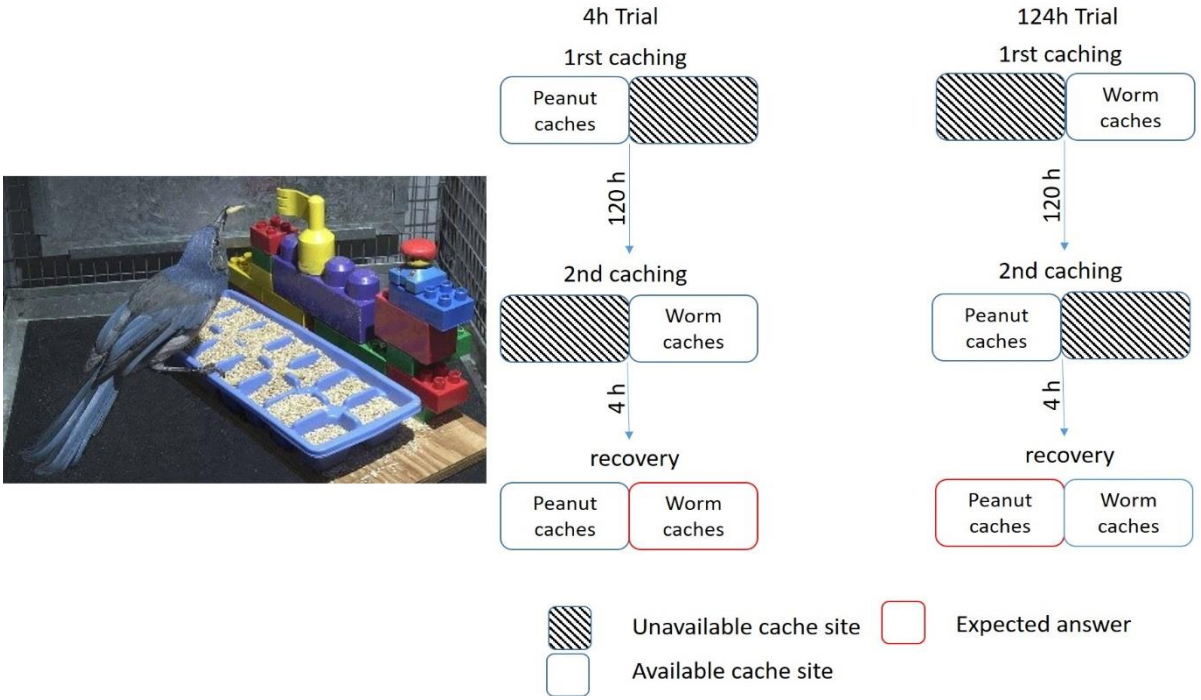

Figure 3 Procedure used in the Clayton and Dickinson (1998) what-where-when task. During the two caching phases, birds can only cache one type of food item, in one of the two sides of the caching tray (the other side being covered). Depending on trials, 4 hours or 124 hours elapsed between the time birds cached their favourite food item (i.e., worms) and time of recovery. Birds are expected to search for worms (favourite food) when 4 hours elapsed since they have been cached, but not when 124h elapsed (worms no more edible).

3. What-Where-When (In Terms of How Long Ago)

Clayton and Dickinson (1998) were the first to experimentally test episodic-like cognition in animals, by using the three behavioral criteria (Figure 3). In their original experiment, California scrub jays (*Aphelocoma coerulescens*) were able to learn that wax worms (preferred food item) would degrade after a long delay (124 h) but not after a short delay (4 h) and that non-perishable food (peanuts, non-preferred food item) would be available at both delays. Birds could cache the worms and the peanuts in a tray during the study phase and then retrieve their caches after 4 or 124h at test. After the short interval, birds searched in the area where they cached the worms, and after the long interval, the jays searched in the area where they cached the peanuts. It seems then that these birds were able to recall what they cached, where, and when. The following studies showed that this result was not due to familiarity cues and that the birds learned the rule by which food would be degraded and how long it would be eatable, forming an integrated representation of the what, the where, and the when. This representation was also flexibly accessed as the birds continued to respond appropriately even when the rule about the delays or the food changed (Clayton et al. 2003b). Recent study showed that magpies (*Pica pica*) were also able to retrieve what was cached, where, and when (Zinkivskay et al. 2009). The episodic-like memory about what happened, where, and how long ago was also investigated in mammals such as rats (Babb and Crystal 2006). In their experiment, the rats

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were trained to discriminate what, where, and when they encountered food. Rats were placed in an 8-arm radial maze where distinctive food (grape, raspberry, i.e., preferred food items) or non-distinctive food (regular chow, i.e., non-preferred food items) pellet was available. During training, rats were allowed to visit four arms and returned after a short or long interval to the maze where all the arms were open. During the study phase, the arms containing chow pellet never replenished until the next trial, while the arms containing grape and raspberry replenished after a long (6 h) retention interval but not after a short (1 h) interval. The arms that were closed during the study phase were filled with chow pellet at test. Results showed that rats were more likely to revisit grape and raspberry locations after long than short delay. Moreover, rats were able to adjust flexibly their behavior when one flavor was devalued. This study showed that rodents are able to encode the content of episodic-like component. Another study showed episodic-like abilities in meadow vole (*Microtus pennsylvanicus*; Ferkin et al. 2008). Male meadow voles can detect when a female is in best disposition for reproduction, a period called postpartum estrus (PPE). In this study, male meadow voles encountered two females in two different locations. One female was pregnant and about to enter the PPE period, while the other was neither pregnant nor lactating. After 24 h, the male was replaced in the same empty maze. At this time, the pregnant female was now a PPE female. The male spent significantly more time in the location of the PPE female. Results also showed that when males encountered a PPE female and a female who was neither pregnant nor lactating during the study phase, at test, males would spend equivalent time in both locations 24 h later as the PPE female was now a lactating female. Thus, meadow vole males were able to remember which female (what) was in the best period for reproduction after a single encounter (when) and in which location he could find her (where). What-where-when abilities were also found in primates (Martin-Ordas et al. 2010). More surprisingly, episodic-like abilities were also found in invertebrates. Cuttlefish are part of the cephalopod mollusk's family. They possess a rich behavioral repertoire making them a good model for investigating complex cognitive abilities. Following the original study of Clayton and Dickinson (1998), Jozet-Alves et al. (2013) presented cuttlefish with similar what-where-when paradigm. On every trials, two distinct emplacements in the tank of the animals were spotted with identical visual cues. When the cuttlefish went close to one of these visual cues, a crab and a shrimp were simultaneously placed in front of the cues. Cuttlefish were then allowed to catch one of the preys. After a short delay (1 h), the non-preferred prey was still available at the previous location, while the location associated with the preferred prey was not rewarded (Figure 4). After along (3 h) retention interval, both locations were reinforced. Results showed that cuttlefish went significantly more close to the visual cue associated with the non-

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preferred prey after a short interval, while they went significantly more to the visual cue associated with the preferred prey after the long interval. Cuttlefish flexibly adapt their foraging behavior according to the delay of replenishment of different preys, which represent the first episodic-like evidence in an invertebrate.

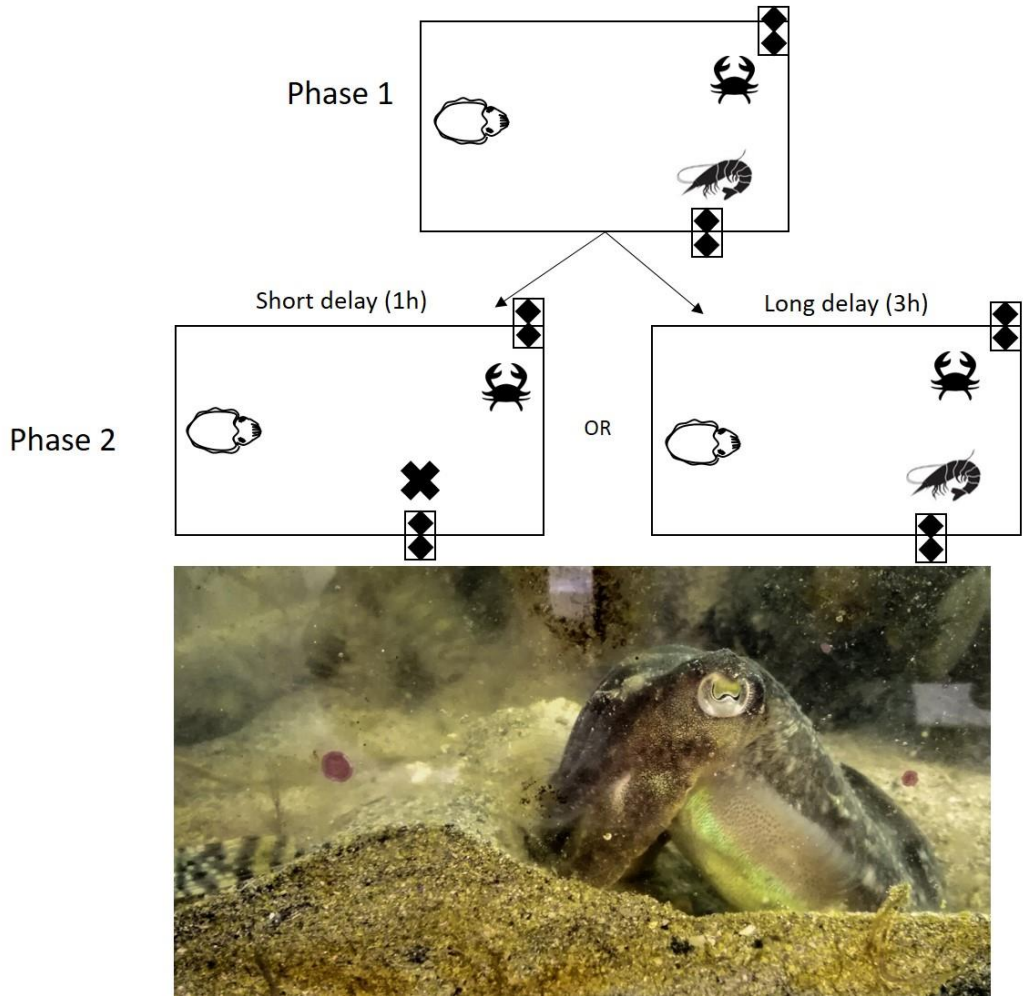

Figure 4 Procedure used in the Jozet-Alves et al., (2013) what-where-when task. Each trial consists of two phases: during Phase 1, the cuttlefish learn which prey is associated to each beacon location; the Phase 2 starts either after a short (1 hour) or a long (3 hours) delay. After the short delay, the non-preferred prey is available but not the preferred prey. After the long delay, both preys are available. Cuttlefish are expected to go to the beacon location associated to the non-preferred prey after a short delay, but to the beacon location associated to the preferred prey after a long delay.

4. What-Where-Temporal Order (Relative Timing)

Another way to investigate episodic-like memory is to consider the "when" component as a relative occurrence of the event. In their study, Fortin et al. (2002) showed that rats could remember series of odors previously encountered presented without any specific spatial cues, while rats impaired with hippocampal lesions showed severe and selective difficulty to recall the sequential order of the series of odors. However, rats with hippocampal lesions were able

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to recall odors that recently occurred. Hippocampus is known to be involved in episodic cognition. Authors argue that hippocampal network is associated with sequential events composing an episodic memory as rats could remember which odors (what) occurred in which order (when) and in which location (where). In another study, rats were trained to remember a sequence of four odors displayed in four different locations on a platform (Ergorul and Eichenbaum 2004). According to the authors, rats were able to recall which combination of odors ("what") was presented in which location ("where") and in which specific order ("when").

5. What-Where-Which

In the original what-where-when paradigm, context was mostly defined as the place and time in which the event took place. Some researchers argue that the "when" component serves to distinguish the remembered event with similar experiences and therefore to context, as opposed to the temporal representation which is important (Eacott and Norman 2004). Thus, the "when" component can be changed into a unique "which" component retrieving contextual information and being comprised in an integrated representation of what-where-in which context episodic-like memory. Moreover, the original what-where-when paradigm relied on natural food-storing habits of scrub jays, and the adaptation of the paradigm with different species can be somewhat tricky. Eacott and Norman (2004) have based their paradigm on the natural tendency of rodents to explore novelty leading to a preference for exploring a novel object over a familiar one. Object recognition tasks are made of two main phases. In the first phase, animals are presented with several objects. In the second phase, a familiar and a novel object are presented at the same time. As rats are neophilic, they will explore significantly more time the novel object instead of the familiar one. In their study, during the test session, rats were presented with two familiar objects in a specific context and location. One of the objects was placed in the same context and location than previously, but the other object was placed in another context and location. Results showed that rats explored more time the object placed in another context and location, showing that rats formed integrated representation of the object, the context, and the location at the encoding. In a more recent study, Eacott and Easton (2007) replicated the what-where-which experiment with another protocol. In their study, rats were placed in an E-shaped maze presented in a specific context (e.g., black). During 3 min, rats could explore the maze where two novel objects (A and B) were placed in the left and right arms. Then, rats were placed in a similar E-shaped maze in a different context (e.g., mesh). Similarly, they could explore the maze for 3 min where the same objects were placed in reverse locations. After this exploration phase, rats were placed for 8 min in habituation chamber with

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one of the object (e.g., A). At test, rats were placed in one of the previous contexts with objects in their context-specific location. Results showed that rats explore significantly more the unhabituated object showing that rats were able to recall what-where-which episodic-like memory (Figure 5). This modified version of the episodic-like memory was also used in domestic animals showing that this cognitive ability is not negatively impacted by domestication. In an adapted version of the what where-which task, domestic pigs (*Sus scrofa*) showed similar abilities to recognize the less familiar object/location/context configuration (Kouwenberg et al. 2009). Episodic-like memory for the context was also showed in zebrafish (*Danio rerio*; Hamilton et al. 2016). Fish were able to remember which object they previously encountered, in which location, and in which context they saw it.

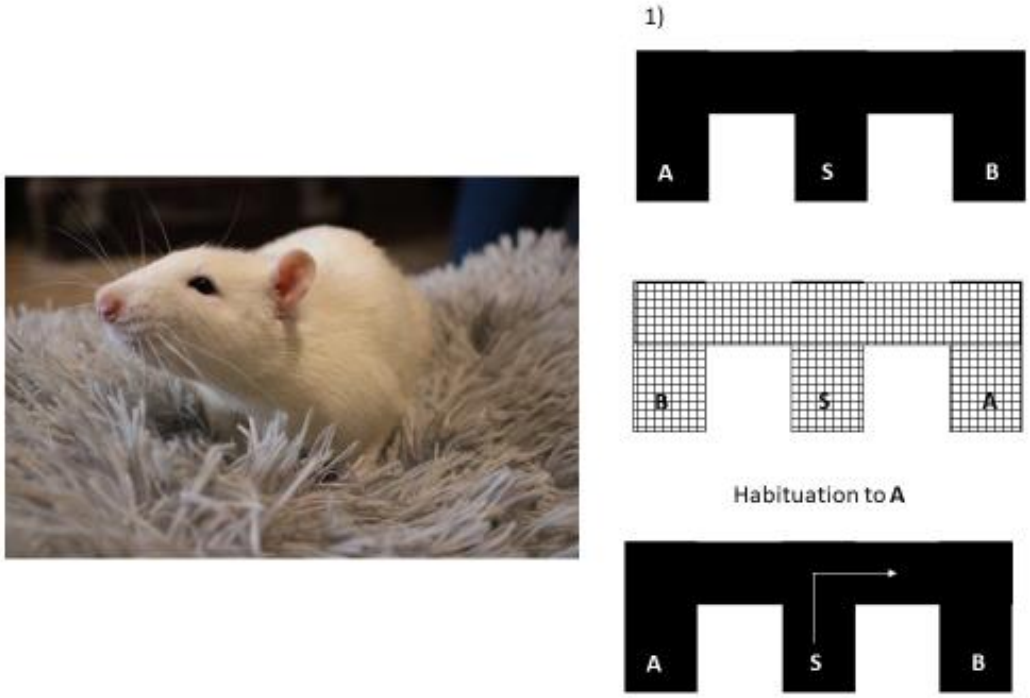

Figure 5 Procedure used in the Eacott and Easton (2007) what-where-which task. Rats were placed in the start arm (S) in the E-shaped maze in one environmental context. After 3 minutes of exploration of two different objects (A and B), they were placed in a second E-shaped maze in a novel context, with the same objects in reversed position for further 3 minutes. Rats were then transferred into a habituation chamber with only one of the two encountered objects (e.g., A) before returning to one of the previous context. Rats are expected to go straight to the arm containing the less explored object (e.g., B in this example) according to the context (they need to turn to the right in the black context, or to the left in the mesh context.

6. Other Ways to Investigate Episodic Cognition

The what-where-when paradigm is now a widely renowned paradigm to investigate episodic like memory. However, other ways are also used to address episodic-like memory. First, some

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researchers question the validity of this paradigm suggesting that it would rely on semantic rather than episodic processes. Indeed, the investigation of episodic-like cognition in animals often depends on rule learning procedures, and researchers argue that animals expect of being asked. It would then be necessary to investigate episodic-like cognition with "unexpected questions" to ensure that animals do not perform a task with semantic information processing. Another way to assess episodic-like memory is to study source-memory which is the ability to retrieve the origin of a memory. Source-memory specifically allows to distinguish between two episodic memories by remembering specific features of the episodic memory which were present when the memory was formed.

Unexpected Question

To ensure that the what-where-when criterion for episodic-like memory is dissociated with semantic memory processes, Zentall and collaborators (2008) suggested to investigate episodic cognition in animals using an "unexpected question." They argue that most research with animals is based on rule learning procedures, such that animals are presented with classical conditional discrimination associated with retention intervals. For the authors, the what-where-when task for animals would actually rely on semantic memory or rule learning instead of episodic memory because animals expect to be asked to retrieve a specific information. In their experiment, pigeons were trained in a conditional discrimination task. Animals had to discriminate between colors (red *vs*. green) and positions (vertical *vs*. horizontal) according to an initial stimulus displayed at the beginning of the trial. Colors were associated with the position of this initial stimulus (e.g., if the initial stimulus was displayed on the left side, pigeons had to peck a red key and inhibit pecking a green key), and position discrimination was associated with the color of the initial stimulus (e.g., if the initial stimulus was yellow, pigeons had to peck the vertical key). At the end of vertical versus horizontal discrimination, if the correct comparison has been selected, pigeons were rewarded by pecking an orange key. At test, pigeons were presented with similar position discrimination task, except that pecking the orange key was followed by red and green key choice. The red and green keys were reinforced equally. Results showed that pigeons remembered the rule associated with the red/green discrimination (i.e., choose the color according to the left/ right location of the preceding stimulus) even though the question was completely unexpected. Other researchers used unexpected questions to investigate episodic memory, for instance, Skov-Rackette and collaborators (2006). They used a what-where-when paradigm asking pigeons in three separate matching-to-sample tasks (old-new recognition task: in matching to-sample tasks, animals are

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rewarded if they respond to a stimulus that was encountered recently; Figure 6). In the "what" task, pigeons had to select the recently presented item. In the "where" task, animals had to select the location where the stimulus was recently presented, and in the "when" task, pigeons had to report how long ago the stimulus was encountered (3 s *vs*. 6 s). Once these tasks were learnt, the pigeons were presented with an unexpected configuration of the experiment in which pigeons had to perform the different tasks in random order. Animals could not expect which tasks or which stimuli were going to happen next. This "unexpected question" paradigm was also used in mammals such as rats which incidentally learned the presence or the absence of food in a radial maze and were unexpectedly asked about it (Zhou et al. 2012).

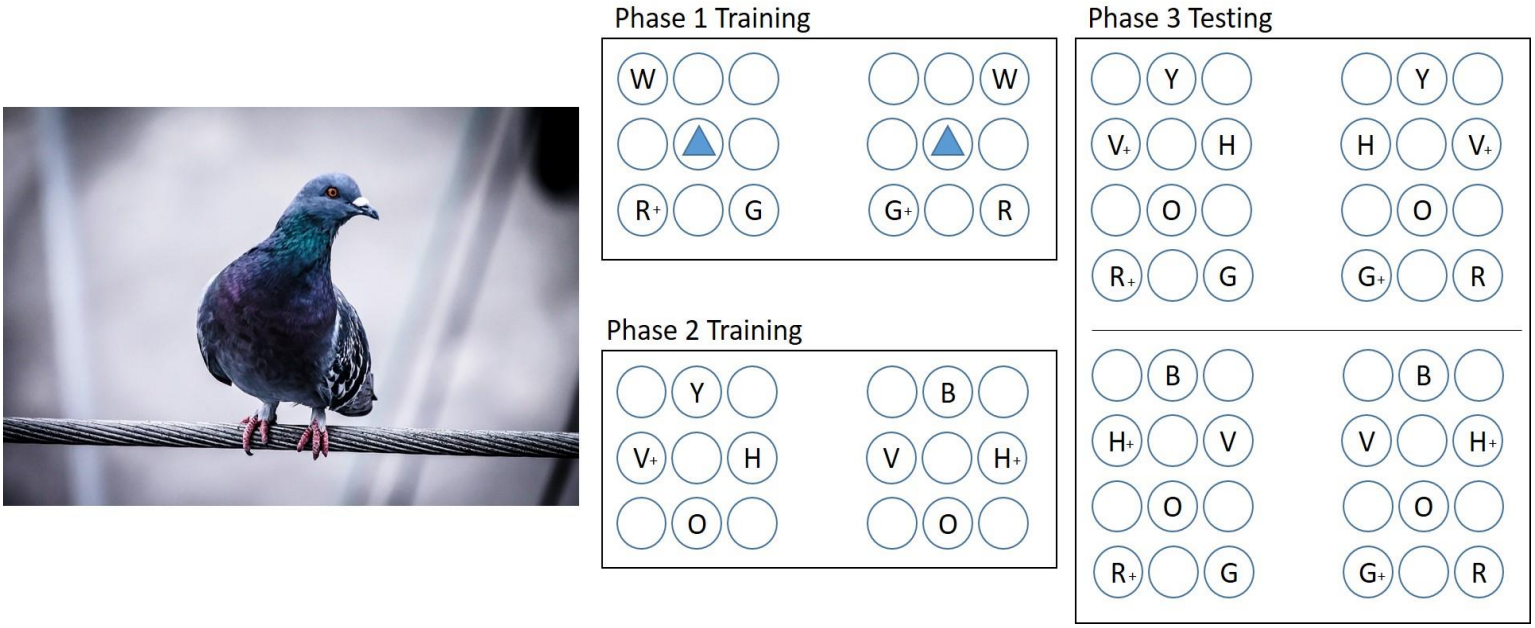

Figure 6 Procedure of the 'unexpected task' designed by Zentall et al., (2008). During the first phase, animals were trained to peck a side key (W) and then to peck a center triangle. If the initial side key was on the left, pigeons had to peck the red key (R+) to get a reward. If the initial key was on the right, pigeons had to peck the green key (G+). The position of the red and green comparison stimuli was counterbalanced. During the second phase, yellow and blue keys were associated with vertical- and horizontal-line comparison stimuli, respectively. Pigeons had to peck the orange key (O) in the center, which was reinforced if the correct comparison had been selected before. Test trials replicated the second phase procedure except that a peck to the orange center key was followed by a choice between a red and a green side keys.

Billard, P., Clayton, N. S., Jozet-Alves, C. (2019). Episodic Memory. In Jennifer Vonk and Todd K. Shackelford (dir.). Encyclopedia of Animal Cognition and Behavior. Springer.

Source-Memory[1]

Another way to investigate episodic memory is to consider the source of the memory, in other words a conscious awareness about how one knows about the informational content of the memory, for example, did I read it or did I hear it? Another way of expressing this idea is to argue that the "memory of the source" allows one to retrieve the origin of the memory by recollecting the information encoded when the memory was formed, constituting the context of the prior situation, and making the memory episodic. Source-memory is essential in everyday life as it contributes to control the reliability of our beliefs, ideas, and memories (Johnson et al. 1993). Troubles in recalling the source of information can be very disturbing and, in the worst cases, lead to delusion and confabulation (the memory of the source contributes to the subjective experience of autobiographical recollection (i.e., the feeling that a memory belongs to one's own past; Johnson et al. 1993). Indeed, the information contained in the memory (e.g., perceptive, contextual, sensitive, cognitive, semantic, affective) allows to relive the event encoded and to recognize the memory as belonging to one's own past. It is important to mention that source-memory is not fundamentally different from episodic memory, but rather it is part of the mental time travel process. (Both are linked such as one leads to the other) When retrieving the source of a memory, the information is not simply accessed, but combined with cue information in an integrated representation, forming the episodic memory (Tulving 1983). The source-monitoring framework of Johnson et al. (1993) describes the processes involved in making attributions about the origins of a memory, knowledge, or beliefs. They postulate that during remembering, records are evaluated and attributed to a particular source through decision processes. These decision processes would allow retrieving of specific features labelling the memory, specifying a memory's source. The ease and the accuracy with which the source of a memory is identified would be determined by the type and the amount of the memory characteristics reactivated in memory records (e.g., spatial, temporal, social context, perceptual, sensitive stimulations, or again cognitive operations), how unique these characteristics are for given sources, and the efficacy of the judgment processes by which sources decisions are made. Some characteristics are less significant than others to recall the source of a memory, depending on the prior situation. For instance, one can remember having been to the beach because he remembers the heat of the sun, the noise of the sea, the persons he was with, or the activities he did. In other words, the perceptive, sensitive stimulations and the social context are really

[1] *As the source-memory part of the published book chapter was quite brief, literature concerning this memory type will be further explained and discussed in the second part of this PhD thesis chapter.*

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significant to recall the source of this information. In another hand, the cognitive operations he performed during the prior situation will be less likely remembered and evaluated to determine the source of this memory. Jonathon Crystal's work with rats constitutes one of the first reports about source-memory in animals (Crystal et al. 2013). In this study, rats had to remember whether they had encountered a preferred food (chocolate) with self-generated cues (i.e., finding the chocolate by themselves) or experimenter-generated cues (i.e., placement of the rat at the chocolate site) cues. When rats found the chocolate by themselves, they had the possibility to retrieve it at the same location, whereas when they were placed by the experimenter in the chocolate location, the latter was not refilled afterward. Rats selectively adjusted revisits to the chocolate location based on source information. When the experimenters temporarily inactivated the CA3 region of the hippocampus with lidocaine, performances during this task were impaired. This result suggests that source-memory is dependent upon an intact hippocampus. Source-memory has also been investigated in great apes with delayed matching to sample procedure where monkeys showed cross-modal recognition abilities of conspecifics (i.e., they confused the identity of a monkey they saw with a monkey they heard; Adachi and Hampton2011) or using item and source-memory dissociation (i.e., monkeys learned to select the image from one source and to avoid the other; Basile and Hampton 2017). However, the study of source-memory in animal is really underrepresented in the scientific community, and there is an urgent need to design behavioral tests to investigate it.

Episodic Future Thinking

In this entry, we have focused on the retrospective component of episodic cognition. Episodic future thinking (or episodic foresight) is the ability to pre-experience (i.e., imagine) or anticipate future personal events. At first, it seems that episodic memory and episodic future thinking represent two opposite sides of mental time travel. However, there is growing consensus that episodic memory is intrinsically linked with episodic future thinking. Scientists argue that the real function of episodic memory would be to increase survival and fitness in present situations and future potential scenario. Thus, episodic memory would not be a memory of the past only but would actually be turned toward the future. Memories are made for the future: that's why they are so labile and flexible and forward-looking. Investigating episodic foresight requires behavioral criterion as well. Behavior will have to be independent of current motivational state to be considered as demonstrating episodic foresight. This criterion is crucial because two identical behaviors can have totally different meaning in terms of episodic foresight. As an example, this morning I went to buy some food because I was hungry; it does

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not represent an anticipation on future needs as my behavior answers a current motivational state (i.e., hunger). However, if I went to buy food while being satiated because I know that I will be hungry in the evening, it can be considered as an episodic anticipation of future needs. The Bischof-Köhler hypothesis postulates that animals always act following current motivational goals, leaving the ability of episodic foresight unique to humans. However, studies demonstrate that animals show future-thinking abilities in a wide variety of domains. As an example, recent studies have shown that rats mentally pre experience navigation and route planning, where hippocampal activations were similar when the rodents travelled through the routes and when they were about to pursue them (Pfeiffer and Foster 2013). Emery and Clayton (2001) showed that jays were able to adjust their caching strategies to reduce the risk of being stolen by a conspecific. Birds could cache food either in private or being observed by another bird. The interesting finding was that birds that have stolen another bird's caches previously then re-cached their food at recovery when they had the opportunity to do so in private, whereas naïve birds that had not experience of stealing from another bird did not re-cache their food. This result shows that re-caching behavior is triggered by previous personal experience of stealing. In other words, birds having stolen from another bird rely on their previous experience of stealing to adjust their caching strategies, which constitutes evidence for future-oriented behavior. After all the only point of re-caching the food is if one is able to recover it at some point in the future. Other studies have shown that Californian scrub jays (*Aphelocoma californica*) would cache the food type that they wished to eat at the time of recovery as opposed to at the time of caching (i.e., their current need is not the same at the time of caching), thereby demonstrating that they could cache with the future in mind and dissociate current from future motivational states (Correia et al. 2007). Subsequent studies with Eurasian jays (*Garrulus glandarius*; Cheke and Clayton2012) demonstrated that these birds could also cache for two future motivational states. Studies of tool use and forethought showed that chimpanzees (Pan troglodytes) and orangutans (*Pongo abelii*) were able to select a convenient tool to obtain a food reward in the future independently of their current motivational state (Osvath and Osvath 2008). Recently, similar findings were found in ravens (*Corvus corax*; Kabadayi and Osvath 2017) and in New Caledonian crows which were able to plan ahead on sequence of tool behavior in metatool problems (Gruber et al. 2019). Taken together, these studies show that corvids can remember specific past events about what happened where and when and can also plan ahead, flexibly adjusting their strategies based on what they predict about what the future will hold, and that they can make these cognitive decisions independently of current desire.

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Conclusion

According to Tulving's definition, episodic memories consist of recollections of what, where, and when a past event occurred (Tulving, 1972). Based on this conception, Clayton and Dickinson (1998) suggested three behavioral criteria for assessing episodic-like abilities in animals, devoid of the complications of the phenomenological characteristics that accompany human episodic memory and are evaluated through verbal report. Clayton and Dickinson (1998) were the first to demonstrate episodic-like behavior in a nonhuman species by developing this what-where-when behavioral paradigm. Subsequent studies have shown that episodic-like memory is found in a wide range of species including mammals, birds, fish, or in vertebrates. Although all of these studies have used a what, where, and when paradigm of some sort, the "when" component has been investigated in multiple ways. Some studies have focused on how long ago the event was encountered following Clayton and Dickinson's original paradigm, while others have studied the relative occurrence of the stimulus (i.e., temporal order; Fortin et al. 2002; Ergorul and Eichenbaum 2004) or the context encoded with the event ("which"; Eacott and Norman 2004; Eacott and Easton 2007; Kouwenberg et al. 2009; Hamilton et al. 2016). Contextual information is specifically investigated in source-memory studies, as source-memory is the capacity to recall the origin of a memory, that is, recalling specific features pertaining to the encoded event (e.g., temporal and spatial location, perceptual, sensitive, cognitive information). Source-memory raises the question of the link between episodic and semantic memory as it involves decision-making processes and judgments about the episodic memory. Some researchers suggest that the what-where-when paradigm involves no more than semantic process, and it has been proven to be difficult to create a what-where-when experiment without rule learning explanation. A possible alternative would be to add an unexpected question as proposed by Zentall et al. (2008) whose aim is to provide animals with a novel configuration of the task, where animals have to use previously acquired incidentally encoded knowledge to formulate an answer (i.e., encoded without the expectancy of being asked). Young children, just like animals, cannot verbally relate their previous past experiences, and researchers need to use a similar behavioural approach to investigate their episodic cognition. Some researchers, for example, Russell and Thompson (2003), have done just this by applying the food caching paradigm (Clayton and Dickinson 1998) and testing preverbal children aged between 14 and 25 months. Their results showed that children between 22 and 25 months could perform the task above chance, reproducing scrub jay performance. Other behavioral studies were used to investigate deferred imitation and source-memory in preverbal children.

Billard, P., Clayton, N. S., Jozet-Alves, C. (2019). Episodic Memory. In Jennifer Vonk and Todd K. Shackelford (dir.). Encyclopedia of Animal Cognition and Behavior. Springer.

Interestingly, these studies show that nonverbal animal tasks can be reliably used with preverbal children, which can help to follow the ontogenetic trajectory of episodic cognition. Taken together, these studies provide evidence that animals do have episodic-like memory. At issue is whether and to what extent episodic-like memory is like episodic memory, in other words whether the ability to remember unique past experiences about what happened where and when involves mental time travel with all its associated phenomenological construes. It is a question that remains controversial, but it is fair to say that the behavioral components of episodic memory, in particular the what-where-when methodology, have led to the development of a comparative cognition approach, from corvids to cephalopods and chimpanzees and from the non-linguistic to the preverbal.

Billard, P., Clayton, N. S., & Jozet-Alves, C. (2019). Episodic Memory. In Encyclopedia of Animal Cognition and Behavior (pp. 1–13). Springer International Publishing. Doi.org/10.1007/978-3-319-47829-6_1770-1

Summary table 1: Exploration of episodic-like memory capacities in animals' species

Species		Authors/years	Procedure
BIRDS			
	*Aphelocoma coerulescens*	Clayton and Dickinson, 1998	What-Where-How long ago
		Clayton and Dickinson, 1999a	What-Where-How long ago / control for simple association between the food types and the cache locations
		Clayton and Dickinson, 1999b	What-Where-How long ago / control for familiarity
		Clayton et al., 2001	Structure criterion
		Clayton et al., 2003	Flexibility criterion
		De Kort et al., 2005	Control for direct forgetting
	*Pica pica*	Zinkivskay et al., 2009	What-Where-How long ago
	*Columbia livia*	Zentall et al., 2001	Did you just peck or did you just refrain from pecking?
	Columbia livia	Zentall et al., 2008	Unexpected question
	Columbia livia	Skov-Rackette et al., 2006	What-where-how long ago; separate retrieval
	*Sephanoides sephaniodes*	Gonzalez-Gomez et al., 2011	What-Where-How long ago
	*Poecile atricapillus*	Feeney et al., 2009	What-Where-How long ago
RODENTS			
	*Long-Evans rat*	Babb and Crystal, 2006	What-Where-How long ago
	Long-Evans rat	Fortin et al.,2002	What-Where-Temporal order
	Long-Evans rat	Ergorul and Eichenbaum, 2004	What-Where-Temporal order
	Dark Agouti rat	Eacott and Norman, 2004	What-Where-Which context
	Rattus (unprecised strain)	Eacott and Easton, 2007	What-Where-Which context
	Long-Evans rat	Zhou et al., 2012	Unexpected question
	Dark Agouti rat	Eacott et al., 2005	What-Where-Which context / control for recollection
	Wistar rat	Kart-Teke et al., 2006	What-Where ; What-When (recency)
	Long-Evans rat	Naqshbandi et al., 2006	What-Where-How long ago (replication of Babb and Crystal, 2005)
	Long-Evans rat	O'Brien and Sutherland, 2007	Pavlovian conditioning of which context-where-when
	*C57BL/6 mice*	Dere et al., 2005a	What-Where-Recency
	C57BL/6 mice	Dere et al., 2005b	What-Where-Recency
	NMRI mice	Belblidia et al., 2015	What-Where-Recency
	*Microtus pennsylvanicus*	Ferkin et al., 2008	What-Where-How long ago

PRIMATES			
	*Pan troglodytes*	Martin-Ordas et al., 2010	What-Where-How long ago
	*Pongo pygmaeus*	Pladevall et al., 2020	FAIL TO SHOW What-Where-How long ago
	*Pan paniscus*		
	*Gorilla gorilla gorilla*	Schwartz et al., 2005	What-Temporal order ; What-Where
	*Macaca mulatta*	Hampton et al., 2005 Hoffman et al, 2009	FAIL TO SHOW What-Where-Wow long ago What-Where-Wow long ago
OTHER MAMMALS			
	*Sus scrofa*	Kouwenberg et al., 2009	What-Where-Which context
	*Canis lupus familiaris*	Fugazza et al., 2016, 2020	Unexpected imitation procedure
FISH			
	*Danio rerio*	Hamilton et al., 2016	What-Where-Which context
INVERTEBRATES			
	*Sepia officinalis*	Jozet-Alves et al., 2013	What-Where-How long ago
	*Apis mellifera L.*	Pahl et al., 2007	What-Where-Which time of day
	*Artificial Intelligence*	Stachowicz and Kruijff, 2011	

II. Source-memory

Introduction

Remember the last time you talked to someone in real life. Can you remember the topic of your conversation, and where and when it was? While you are trying to remember these elements, you may deliberately or unintentionally remember other details such as the emotional value of the conversation (e.g., was it nice, fun, or were you angry or sad?), some perceptual features (e.g., the way your interlocutor was dressed, the colour of the room, of the environment), semantic information (e.g., specific information, associated item), or again the cognitive operations engaged (e.g., the conversation required you to think carefully to understand the subject). These details bound together form a mental representation of the past event: the episodic memory. More specifically, these details give the memory its episodic character (Johnson, 2006), and allow to distinguish between two or more episodic memories (Mitchell and Johnson, 2009). Each of these features can be used to attribute the episodic memory to a particular source (e.g., in this example retrieving the name of the person you talked to earlier).

1. What is source-memory?

The memory of the source is the ability to retrieve the specific features composing an episodic memory and make an attribution about its origin (Johnson et al., 1993; Mitchell and Johnson, 2009). It is an essential ability in everyday life, allowing us to form judgements and beliefs (e.g., in the example presented above, it can be to decide whether the information transmitted by the person is likely to be trusted or not; Craik et al., 1990; Dobbins et al., 2002; for a recent review on the crucial role of episodic and source in humans see Mahr and Csibra, 2020). Source-memory creates a coherent mental representation of a past event (Moscovitch, 1994), allowing to mentally re-experience it. An impairment of source-memory can lead to false memories, and confabulation that can have dramatic consequences in certain circumstances (Loftus and Hoffman, 1989; Lindsay, 1994; Zaragoza et al., 2007). For instance, researchers evidenced that witnesses can be unconsciously influenced by post-event information that will distort their memories and report false information in criminal investigations (e.g., Brewer and Burke, 2002; Brewer and Wells, 2011; for a review on the suggestibility of human memory see Steffens and Mecklenbräuker, 2007). This lack of source-memory (called the *misinformation effect*), was reproduced experimentally with the misinformation paradigm. In this paradigm,

participants witness an event (e.g., a man slipping a stolen wallet in the pocket of his jacket), then they are presented with misleading information (e.g., the man slipping the wallet in the pocket of his pants). Finally, the participants are asked to answer to questions about the original event (e.g., Loftus et al., 1978; Zaragoza and Lane, 1994; Lindsay et al., 2004; Okado and Stark, 2005). Although source-memory can be impaired by different mental illness such as dementia (Multhaup and Balota, 1997); amnesia (Shimamura and Squire, 1987); or frontal lobe disease (Glisky et al., 2001), it can also be impaired during physiological ageing (Spencer and Raz, 1995). These source-memory impairments can be explained by the fact that source-memory involves reconstructive and decision processes whose efficiency can decrease with age (Bröder and Meiser, 2007).

Source-monitoring refers to "the set of processes involved in making attributions about the origin of memories, knowledge, and beliefs" (Johnson et al., 1993, p. 3). To describe these different processes involved in source-memory, researchers created the conceptual framework called the *Source-Monitoring Framework* (SMF; Johnson and Raye, 1981; 2000; Johnson et al., 1993; Johnson, 2006; Lindsay, 2008; Mitchell and Johnson, 2009). This framework illustrates the associative mechanisms by which the features of the memory are bound together during the encoding and the retrieval, and the decisional processes involved when making the attribution of the source to a specific event (Johnson et al., 1993; Mitchell and Johnson, 2009, Figure 7). Authors distinguish three different types of source-monitoring (Johnson et al., 1993): the external source-monitoring which concern the ability to discriminate between two or more external sources of information (e.g., information heard on the radio or told by a neighbour), the internal source-monitoring which concern the ability to differentiate between internally generated information (e.g., did I say it or did I think about it?). Finally, the internal-external source-monitoring (also called reality monitoring) concerns the discrimination of information from internal and external sources such as memories for perceived events and memories for thoughts and imagination.

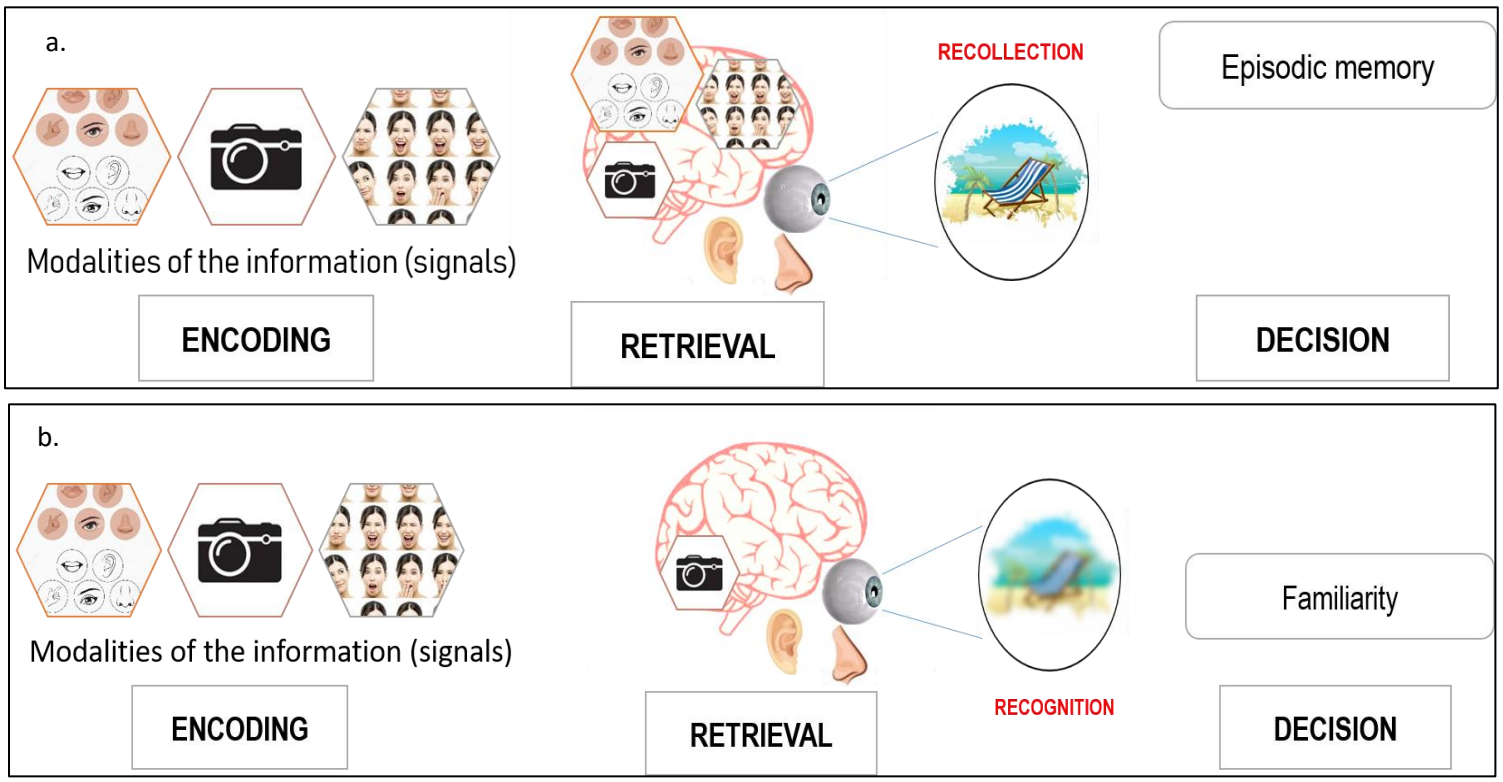

Figure 7 Theorized by Johnson et al. 1993, the source-monitoring framework proposed a modelling of human's source-memory processes. Signals are encoded when the subject witnesses the event. These signals are reactivated at retrieval. If enough of the signals are reactivated, the mental representation of the memory will be clear and the source of the episodic memory will be retrieved by recollection (Figure 7a). If not enough of the signals are reactivated, the mental representation of the memory cannot be formed clearly. In this case, the subject need to determine the source of the memory by familiarity and recognition (Figure 7b).

When witnessing an event, the features composing the event (also called signals of information) are bound together at the encoding to form a coherent representation of the event (Moscovitch, 1994). Depending on the level of attention, the number and the quality of the signals encoded are variable. The higher the number of signals encoded and retrieved, the better the quality of the mental reactivation of the event. For instance, stress can sometimes increase the quality of the encoding of episodic memories (e.g., Payne et al., 2007). If the witness' attention is focused on the event, its signals can be deliberately encoded, but usually they are encoded incidentally (i.e the signals are encoded without knowledge that they might be important later).

At retrieval, these signals are reactivated and they need to be bound together again to evoke an integrated representation of the past event. Failure in this binding mechanism or in the quantity of features reactivated during the retrieval will cause the inability to recollect the episodic memory (Johnson et al., 1993). Depending on the quality of the encoding and the retrieval, the quantity and quality of the signals remembered can differ. According to the SMF, the *vividness* of the revived features can vary, which means that the representation of the

memory will be more or less detailed and clear (Mitchell and Johnson, 2009). When a sufficient amount of signals is retrieved, the mental representation of the memory will appear clearly in the brain (i.e., high level of vividness), allowing to identify the source of the event: this is the recollection of the memory (Figure 7a). The authors said that in this case, the association of features retrieved is well *differentiated*, which means that it is very specific to a particular event. When not enough features are bound together (low differentiation), the level of vividness is low, giving a vague and blur memory representation. In this case, the representation of the event gives a vague feeling of familiarity (i.e., I know that I talked with a woman, but I cannot remember who it was; Figure 7b). Some features are more significant than others to recall the source of a memory. For instance, the perceptive signals (e.g., the sand was very hot) are more significant to recall the source of the event "arrival at the beach last week-end" than the cognitive signals (e.g., I was thinking about my next birthday when I just stepped on the sand).

The SMF also describes the decisional processes involved in the identification of a subjective experience as being a trustworthy representation of a past event. Indeed, once the signals are retrieved, records are evaluated and attributed to a particular source through decision processes. Sometimes, the source is automatically retrieved, because the features are sufficient and well differentiated to trigger its recollection. But sometimes, additional information is needed to remember the source of the information (Johnson and Ray, 1981). For instance, you can remember that you talked with someone about an upcoming storm earlier, but you cannot remember who it was (e.g., was it your colleague or your neighbour?). To retrieve the source, you might then remember where you both talked (e.g., was it at work or in your garden?) to obtain another clue on this memory. This complementary information will then allow you to decide which of the two persons you talked to earlier (e.g., it was my neighbour because I remember we talked next to her car in our alley this morning before going to work).

To sum up, according to the SMF, the successful retrieval of episodic memory would depend on the type and the richness of the memory features reactivated in memory records, how unique these features are for given sources, and the efficacy of the judgement processes by which sources decisions are made.

It is important to note that episodic memory and source-memory are not fundamentally different classes of memory (Johnson, 2005; Mitchell and Johnson, 2009). On the contrary, both seem to be intrinsically linked to the other: on one hand, we can mentally relive an episodic memory if the processes involved in source-memory are activated (i.e., retrieving the episodic

memory implies to retrieve the features composing the memory which is comprised in source-monitoring processes). On the other hand, retrieving the source of an event implies to reactivate the episodic memory of this event.

2. Source-memory investigation in humans

In humans, the classical task to investigate source-memory is the *item vs source task* (also called *source recognition task*) that has been largely documented in the scientific literature. This task opposes the ability to retrieve an item (item memory) to the ability to retrieve the context (i.e., source) in which the item was previously encountered (source-memory; e.g., Jurica and Shimamura, 1999; Davachi et al., 2003; Mitchell et al., 2006; Sprondel et al., 2011). It is important to note here, that what is referred to as "context" in source-memory encompasses and subsumes what is often called "context" in episodic memory (i.e., spatial and temporal information). Indeed, the source-memory "context" refers to all the features (spatio-temporal information and others) that were present when the episodic memory was formed (Mitchell and Johnson, 2009).

During the study phase of these experiments, participants are presented with a list of items that can be for instance: words (e.g., Pergolizzi and Chua, 2016; Elekes and Sebanz, 2020; Jeon et al., 2020, McCurdy et al., 2020), images (e.g., Petten et al., 2000; Cycowicz et al., 2001; 2003), faces (e.g., Lee et al., 2019), voices (e.g., Glisky et al., 1995; 2001), objects (e.g., Ventura-Bort et al., 2020; Stevenson et al., 2020), abstract visual shapes (Slotnik et al., 2003), etc. After a delay, in the test phase, the previously encountered items are mixed with new ones, and item memory is evaluated by asking participants whether the item presented is "old" or "new" (i.e., whether the item was encountered during the study phase or not). When an item is considered as "old", the participants are asked to retrieve the source associated with the item. Indeed, the items belonged to different sources such as different lists (e.g., Wegesin et al., 2002), different categories (e.g., "bigger/smaller than a shoebox" or "living/non-living", Gruber et al., 2008), different colours (e.g., Doerksen and Shimamura, 2001), different genders (e.g., Unsworth and Brewer, 2009), different locations on a screen (e.g., left or right, Duarte et al., 2004; top or bottom, Mieth et al., 2019; the corner of apparition of the *stimuli*, Unsworth and Brewer, 2009), etc. For instance, participants presented with series of different visual shapes during the study phase, were then asked to judge whether these shapes intermixed with new shapes were old or new (item memory). During the source-memory phase, participants had to

retrieve whether the old shapes originally appeared on the left or on the right side of the screen (source-memory, Slotnick et al., 2003).

3. Source-memory investigation in animals

Source discrimination

Only few studies have investigated animal's capacities to remember the source of an event. The most striking evidence comes from Crystal and collaborators who developed a behavioural paradigm to test source-memory in rodents (Crystal and Alford, 2013; Crystal et al., 2017; Smith et al., 2016; for review see Crystal 2016, see also Crystal 2018). In their first study, rats showed that they were able to distinguish between self-generated information (i.e., I discovered this information by myself) and experimenter-generated information (i.e., the experimenter showed me this information; Crystal et al., 2013, Figure 8). During the study phase, rats were placed in a radial maze, containing chocolate pieces distributed in two randomly selected arms (the other arms containing chow pellets). Rats find the chocolate through the help of the experimenter who places them directly in one of the two arms containing the chocolate and by themselves while exploring the maze. If the rats had to found the chocolate by themselves during the study phase, it was replenished during the following test phase, while if the rats were placed by the experimenter in the arms containing the chocolate, it was not replenished during the following test phase. Results showed that rats revisited significantly more the chocolate locations when their discovery was self-generated than when it was experimenter-generated. They were then able to distinguish whether they learnt the information by themselves or whether this information was shown by someone else. Later, the authors showed that the findings were not due to an "encoding failure" where the rats would have encoded only some part of the information, solving the task *via* associative processes instead of creating an episodic memory (Crystal and Alford, 2014). More specifically, rats can remember the source of an information at least seven days. At the same time period, they also showed that like humans, rats use a bond representation of their episodic memories and are able to distinguish multiple episodes (different chocolate encounters) sharing some similar features (Crystal and Smith, 2014).

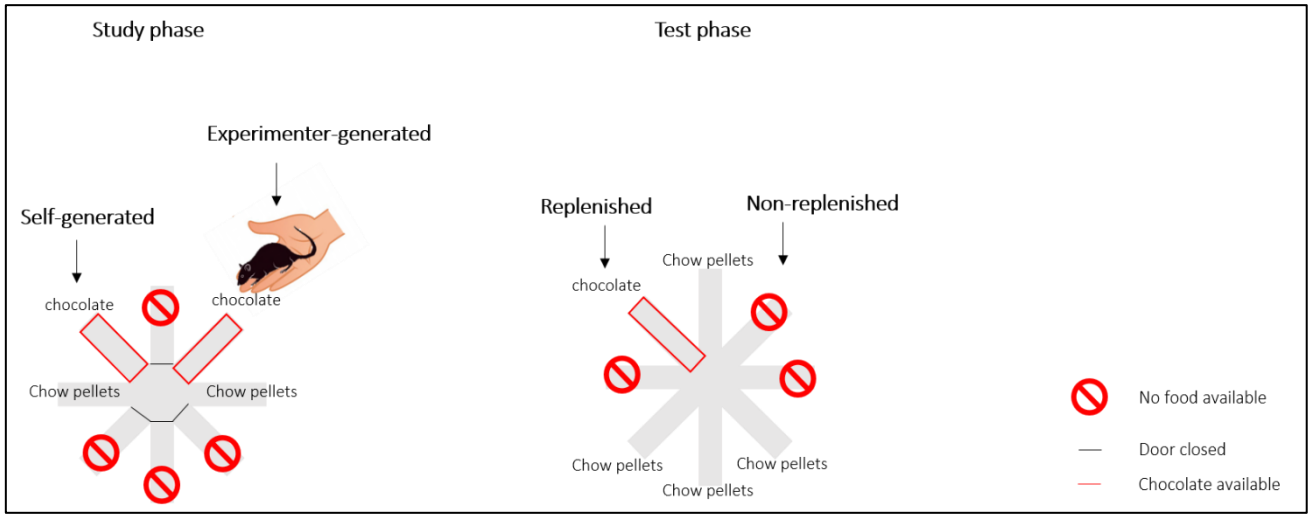

Figure 8 Procedure of the source-memory task designed by Crystal et al., 2013.

Source-memory was also investigated in primates. This study used item *versus* source-memory task inspired by the procedure used in humans (Basile and Hampton, 2017, Figure 9). Rhesus monkeys (*Macaca mulatta*) were able to distinguish images according to the task they had to perform (i.e., I know the picture because I needed to touch it on a screen or to classify it). In the first experiment (classify *versus* touch discrimination training Figure 9.1), monkeys were first presented with a picture on a screen (a bird, a fish, a flower, or a person), that they were asked to touch to go to the next step of the trial. After a short delay, they had the opportunity to classify a picture by touching one out of four symbols situated on each corner of the screen (each geometrical shape being associated to a different category: bird, fish, flower or person). In the subsequent memory test, the touched picture, the classified picture, as well as two distractors were displayed on the screen. When monkeys selected the touched image, they were rewarded with food. When monkeys selected any other images a negative audio cue was displayed. In the second study, to make sure that monkeys did not learn to choose the first image encountered rather than discriminating the pictures based on their sources, the order of appearance of the pictures which need to be classified and touched was switched (Control of the temporal order of the items, Figure 9.2). In the third experiment (classify versus touch discrimination depending on background colour, Figure 9.3), the colour of the screen background changed randomly during the test phase. Each colour (either blue or brown) was indicating whether the monkey needed to select the previously touched or the previously classified picture to get a reward. Monkeys managed to select the touched image even when the conditions were reversed, and to select either the touched or the classified images when presented with the corresponding background.

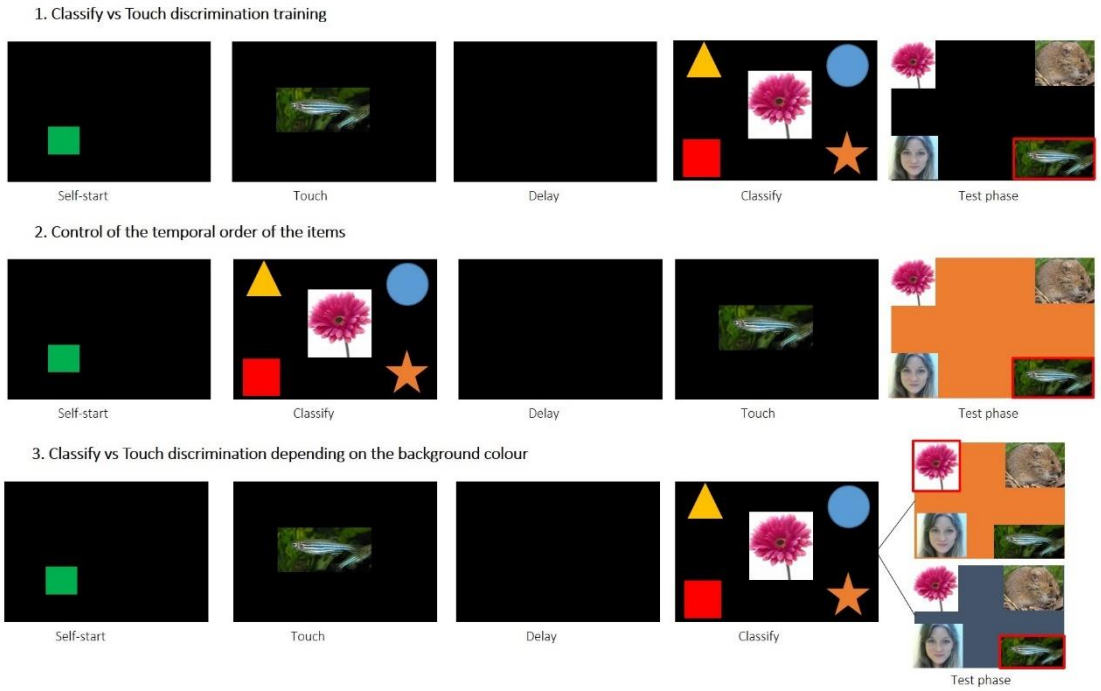

Figure 9 Procedure of the item vs source task designed by Basile and Hampton, 2017.

Incidental encoding

Source-memory is linked to episodic memory by nature, because the episodic recall of an episodic memory implies source-memory processes. One defining characteristic of episodic memories is that they can be remembered even if their encoding was not deliberate (i.e., not encoded on purpose), namely incidental (Zentall et al., 2001, 2008; Singer and Zentall, 2007; Zhou and Crystal, 2011; Zhou et al., 2012). Thus, an information incidentally encoded can be retrieved only if it implies source-memory mechanisms.

In most episodic-like memory tasks designed to test animals, individuals are trained to learn a rule. These trained individuals might then know which feature of an event will be needed to successfully solve the upcoming memory test. For instance, in the seminal episodic-like memory paradigm, jays are trained to learn that worms always decay after a long delay while peanuts are always fresh (Clayton and Dickinson, 1998). The jays are trained and tested the same way: they cache worms or peanuts, and after a short and a long delay they have the opportunity to look for the previously cached food items. When the animals are caching food, they might deliberately encode information for the upcoming memory test and generate a planned action (Zentall et al., 2001; Zentall, 2005; 2006; Singer and Zentall, 2007; Zentall et al., 2008; discussed in Crystal, 2018). Thus, animals may be able to solve the task without

remembering earlier episodes (i.e., without episodic memory), but using a learned semantic rule (i.e., short delay=worms, long delay=peanuts).

One solution to be sure that animals are not creating expectations on what is going to be asked, is to use an incidental encoding paradigm and/or an unexpected question (Zentall et al., 2001; Singer and Zentall, 2007; Zentall et al., 2008; Zhou and Crystal, 2011; Crystal 2013). When the information is encoded incidentally and/or, when animals do not know that it might be important to save a particular information for later, it is not possible that the animals develop expectations about what is coming next (Cyrstal, 2018). The only way for the animals to successfully solve the unexpected memory test is to retrieve an episodic memory of the earlier event (Zentall et al., 2001, 2008; Singer and Zentall, 2007; Zhou and Crystal, 2011).

Animal cognition literature has evidenced the use of the unexpected question after incidental encoding. Zentall and colleagues have for instance demonstrated that pigeons possess episodic-like memory abilities using an unexpected question (Zentall et al., 2001, 2008; Singer and Zentall, 2007; see Other Ways to Investigate Episodic Cognition, p.11). Incidental encoding and unexpected question was also used in rats (Zhou et al., 2012, Figure 10). The animals were trained to perform two tasks in the same eight-arm radial maze apparatus. In the first task, rats foraged for food in five out of the eight arms. In the study phase, three out of the five arms provided a food pellet. In a subsequent foraging phase, the two arms that did not provide a food pellet were baited with a food pellet. In the second task, the rats had access to only three out of the eight arms of the radial maze, representing a T-maze. They were placed in one arm where they obtained food (six pellets) or no food (zero pellet). Then, they had the opportunity to go either in the left or the right arm. They were rewarded for selecting the arm associated with the previously encounter with food or absence of food (e.g., left=food; right=no food). During the unexpected question, the rats foraged for food in the five arms in the study phase. They were then placed in the T-maze arms were they had the opportunity to report whether they previously encountered food. Thus, the two tasked were unexpectedly linked in one single task. Rats could not expect that they would have to encode the presence of food or no food in the first task because they were never trained to do so. To correctly choose the left or the right arm in the T-maze, they must have incidentally encoded the presence or absence of food in the first foraging phase in the five arms.

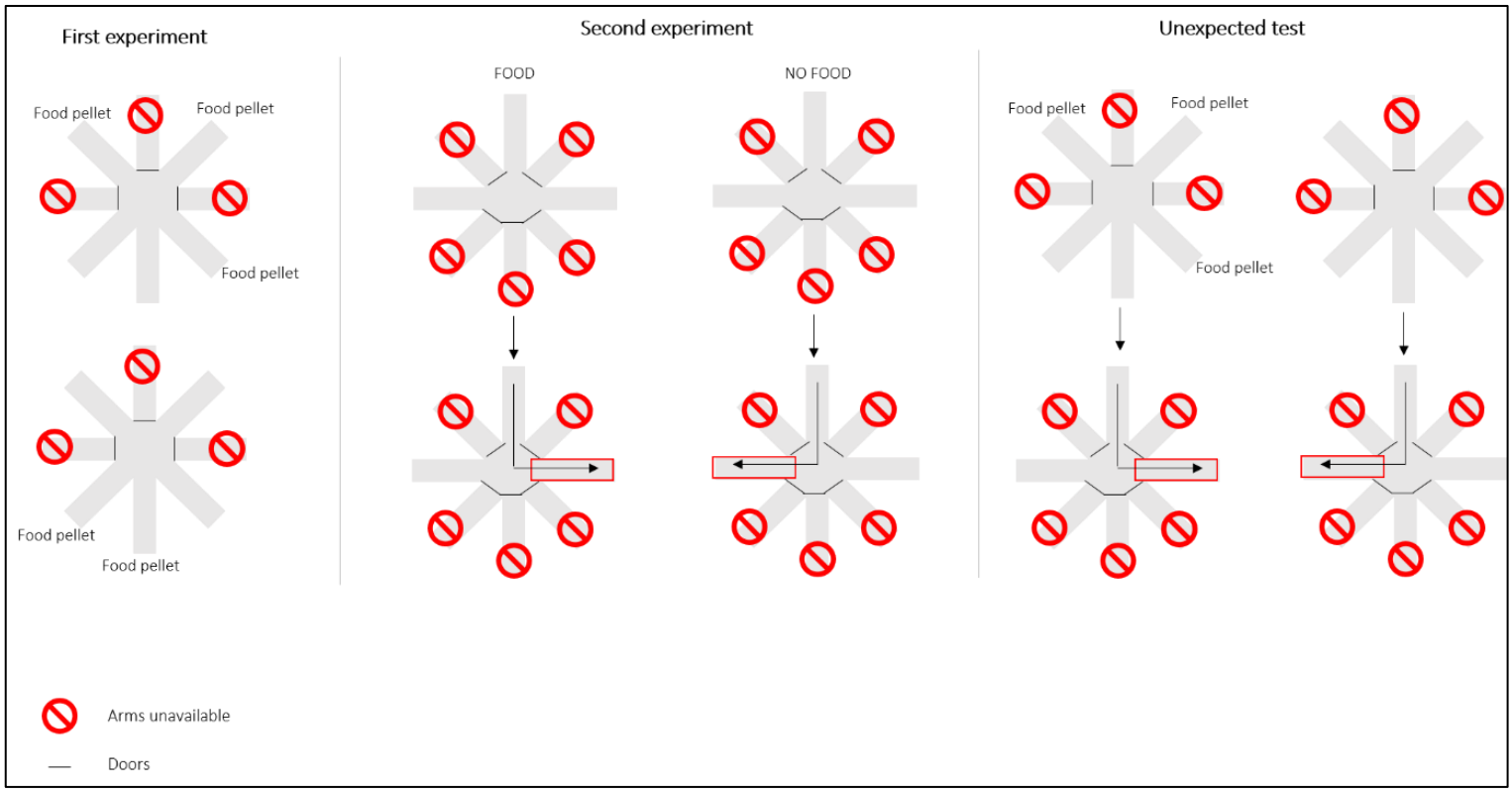

Figure 10 Procedure of the incidental encoding task designed by Zhou et al., 2012.

Several other studies have investigated animal's capacity to incidentally encode information (e.g., Goldberger et al., 1980; Fujita et al., 2012; Fugazza et al., 2016, 2020; Takagi et al., 2017; Sluka et al., 2018; Allen et al., 2020), however, often the to-be-remembered item is the centre of attention at the time of encoding (i.e., the animals are trained with the object of the incidental encoding) and it is possible that animals deliberately encoded it instead of incidentally (for further discussion on this subject, see Chapter 2, *Eurasian jays show sex differences in simple discrimination learning and incidental encoding* of the thesis). Thus, it would be relevant to propose a new way of testing incidental encoding in animals, where the object to incidentally encode is not the focus of attention during training. That way, if the animal is able to retrieve the incidentally encoded information, it would mean that source-memory mechanism underlies the retrieval of the incidental information.

Summary table 2: Source-memory in animals

Species	Authors/years
RODENTS	
 *Long-Evans rat*	Crystal et al., 2013 Crystal and Alford, 2014
PRIMATES	
 *Macaca mulatta*	Adachi and Hampton, 2011 Basile and Hampton, 2017

B. Comparative study of episodic cognition

I. Comparative cognition

Introduction

Defining cognition has been proved to be very challenging and there is no one agreed definition of it (Allen, 2017; Bayne et al., 2019). In this PhD thesis, I will use a very broad definition of cognition that gathers all the aspects of information processes (from the senses to the brain). Cognition refers to information processing, from gathering information through the senses to decision making on actions to perform, regardless whether this information processing is conscious or not (Clayton *in* Bayne et al., 2019; Shettleworth, 2000). Cognition is inherently linked with the way animals perceive their environment, and asking how an animal processes information is asking what the animal can detect (e.g., see, smell, or hear) from a given situation. Thus, researchers must take into account the type of environment in which animals are living, and the ecological pressures that animals are facing (e.g., predation, reproduction) to investigate cognition in different species.

Comparative cognition is a subfield of comparative psychology, aiming at uncovering the cognitive continuity between species. Nowadays, it typically focuses on two main issues: first determining whether animals present cognitive processing mechanisms allowing a flexible use of information which would not be likely explained by basic associative learning mechanisms. Secondly, studies focus on the evolution of cognitive processing, to evaluate whether similar cognitive processes have evolved convergently in distant species exposed to the same selective pressures or whether they have evolved independently in species that have been exposed to different environmental constraints (Clayton *in* Bayne et al., 2019). Comparative cognition has not always focused on animal capacities *per se*. Originally, it emerged to establish the differences and similitudes of psychological abilities and characteristics of the mind between humans and non-human animals. Today, this anthropocentric framework is contested in favour to a non-human centred framework considering species-specific abilities in relation to their ecological context (e.g., Shettleworth, 2012; Eaton et al., 2018; Bräuer et al., 2020).

To fully understand the evolution of the field, we need to go back 150 years in the past history with the creation of Psychology (1879; Beran et al., 2014) and with the creation of Darwin's theories (1871, 1872) on animal mind and behaviour. However, comparative cognition emerged as a scientific field only recently, under the influence of eminent researchers

such as Tinbergen, Lorenz or Von Frish, and the publication of *Cognitive Processes in Animal Behaviour* by Hulse, Fowler, and Honing (1978; Wasserman and Zentall, 2006).

1. A little bit of history

When Darwin wrote his famous books *The Descent of Man and Selection in Relation to Sex* (1871) and *Expression of the Emotions in Man and Animals* (1872), he made it clear that his agenda was to document the cognitive continuity between non-human species and humans. His view was anthropocentric, which means that his studies of animal behaviour were based on the search of human-like abilities in animal behaviours. His writings inspired lots of naturalist researchers and others (e.g., pet owners, zookeepers) who then described animal behaviours by using anthropomorphic interpretations (what I refer to later as the "anecdotal method"), suggesting that natural behaviours displayed by animals should refer to similar human psychological processes (Wasserman, 1993; Shettleworth, 1993; Wasserman and Zentall, 2006). For instance, Romanes (Darwin's student) described a cat which managed to open a door: "First the animal must have observed that the door is opened by the hand grasping the handle and moving the latch. Next she must reason, by 'the logic of feelings'—If a hand can do it, why not a paw?" (Romanes, 1892, p. 421). Animals witnessed to solve complex problems were assumed to use very complex reasoning (such as "insight" for instance, which is the sudden understanding of an explicit knowledge and causal reasoning; Sternberg and Davidson, 1995), even though it was later showed that animals could solve similar problems using simple associative processes (Povinelli et al., 2000).

Such impartial assumptions about the mechanisms and the development of behaviour have raised the question of subjectivity in the observation and the study of animal behaviour. Notably, Morgan (1894), another psychologist interested in evolution and animal behaviour rejected the anecdotal method (i.e., the subjective/anthropomorphic description of animal behaviour) as a comparative cognition science and pointed the fact that science must be objective and replicable. He wrote what is known as "Morgan's canon" (Morgan, 1894), where he exposes the rules that would prevent the bias of anthropomorphism[2]: "In no case may we

[2] Today, "anthropomorphism" refers to a mistake or an intellectual failure of attributing psychological human characteristics to animals. More recently was raised the focus on a second mistake at the opposite of the first one: anthropodenial (De Waal, 1999; Sober, 2005), which is the tendency to deny the existence of human-like characteristics in animals. A probably better approach to parsimony would be situated in-between anthropomorphism and anthropodenial, such as evidentialism, which assumes that we should only accept what we have good evidence for (i.e., don't state that animals present lower or higher cognitive processes unless you have good evidence for it, Shettleworth, 2012; Fitzpatrick, 2008; Sober, 2005). It should not be

interpret an action as the outcome of the exercise of a higher psychical faculty, if it can be interpreted as the outcome of the exercise of one which stands lower in the psychological scale." (Morgan, 1894, p. 53). Morgan's canon was discussed recently because it implies to classify hierarchically cognitive faculties to determine which cognitive ability is "higher" and which cognitive ability should be considered as "lower" (Sober 2005; Shettleworth, 2012). Thus this view is disputed because it is based on anthropocentric viewpoint[3] (e.g., Bräuer et al., 2020) and can lead to claim that a given species is more "clever" than another because it displayed a behaviour revealing a human-like cognitive ability. A more relevant viewpoint to avoid any hierarchy of the cognitive abilities observed in animals, would be to reason in terms of ecological relevance of one given behaviour or some cognitive skills in one animal species (i.e., biocentric perspective, Bräuer et al., 2020). Morgan's canon was then reinterpreted in what is called the cladistics parsimony (Sober, 2005, Cabrera, 2017). This new parsimony theory states that if all species tested present basic abilities (even invertebrates) then these processes must have evolved early in evolution, and thus are present widely in the animal kingdom (Sober, 2005; Shettleworth, 2012).

Following Morgan's canon, the well-known researchers Thorndike (1874/1949) and Pavlov (1849/1936) developed highly reliable and objective research methods. The behaviourists (such as Watson, 1913) stated that it was absurd to infer any mental processes to explain animal behaviour because they are not measurable. They relied on observable behaviours to explain animal behaviour. Their highly controlled experimental methodologies considerably improved experimental research in comparative cognition. Skinner (1930) developed his "box paradigm" testing behavioural responses under simplified and controlled experimental conditions. Behaviourism set the basis for experimentations, and the anthropocentric approach of animal behaviour's investigation was put aside for many years.

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assumed that because one animal does not present a given capacity during a test, it does not possess it at all. A lot of reasons can explain that an animal did not perform well on a task: the task itself might have failed at evidencing the expected capacity for instance.

[3] Apart from the methodology used to investigate animal behaviours, the anthropocentric approach presents several other weaknesses. By searching for human-like behaviours in animals, researchers are missing some crucial and rich behaviours in animals. Placing humans as model for studying and assessing animal abilities narrows the range of topics studied and biases the explanations of behaviours. It leads to consider that some species are cleverer than others because they seem to reflect human's mental processes and orient the type of species studied.

In the 30's, another school of animal behaviour advocating objective and reproducible studies emerged: the discipline of ethology. This discipline focussed on spontaneous animal behaviours in their natural habitats (Wynne, 2007). Tinbergen (1963), identified four questions to investigate animal behaviour: its proximal cause (i.e., the proximal cues that elicited it as for instance the sight of a predator caused the animal to freeze), its developmental history (the freezing behaviour emerges early during ontogenesis in mice), its current function (freezing can improve hypervigilance and thus prepare a motor response; Bracha, 2004; Leach, 2004), and its evolution. In 1973, he received the Nobel Prize of Medicine with Lorenz and Von Frish for "their discoveries concerning organization and elicitation of individual and social behaviour patterns" (The Nobel Prize in Physiology or Medicine, 1973). Contrary to Darwin, their central focus was on animals *per se* and not on their relation to humans. More specifically, they were interested in how animals act in their natural environment and evolutionary context. This approach is sometimes referred to as the ecological approach of animal behaviour (Kamil and Mauldin, 1988; Shettleworth, 2012). It allowed broadening the scope of the type of species studied from mammals to insects, birds, fish (Burkhardt, 2005).

The comparative cognition field really started at this time of history, with the resonance of the behaviourist controlled methodology, and the writings and the recognition of the work of Tinbergen, Lorenz, and Von Frish. In 1978, was edited the book *Cognitive Processes in Animal Behaviour* (Hulse et al., 1978), marking the beginning of the field (Wasserman and Zentall 2006; Shettleworth, 2009; Shettleworth, 2012). Although behaviourists considered the mind as a black box or a computer, attention was then given to what was happening inside, such as memory, attention, learning, time understanding, and use of concepts. Today, the study of cognitive processes encompasses much more topics and species than before (Shettleworth, 2010), and includes different approaches: e.g., behavioural ecology (see Healy et al., 2008, Cuthill, 2005); cognitive ethology (see Griffin and Speck, 2004, Dukas and Ratcliffe, 2009); sensory ecology (see Endler and Basolo 1998); evolutionary comparative cognition (see Galef and Heyes, 2004). The involvement of a wide range of researchers (e.g., ethologists, ecologists, anthropologists, psychologists and even philosophers) provides a great richness to the field but also leads to debates and controversy.

2. Current issues of comparative cognition

Shortly after Hulse and collaborators (1978) writings, some researchers pointed that: 1) comparative cognition science should investigate a wider range of cognitive abilities in animals

such as the cognitive processes used to solve problems in natural environments, and 2) that a broader range of species should be included in these studies (Kamil 1987; Kamil and Mauldin, 1988; Shettleworth, 1993). These critics were already made years before, against the comparative psychology research (e.g., Beach, 1950; Bitterman, 1960), where most studies included only rats as subjects (Bitterman, 1960). Although these critics were made more than 50 years ago, recent reviews showed that some species still stay underrepresented (e.g., invertebrates) and some are still overrepresented (e.g., primates, rats and pigeons; see Beran et al., 2014 for the time period 2001-2010; and Shettleworth, 2009 for the time period 2005-2007). In the meanwhile, the number of studies in comparative cognition has exploded in the last 20 years with an increase number of citations of about 10 times between 2000 and 2019 (400 citations in 2000 and 4000 citations in 2019; Bräuer et al., 2020; Figure 11).

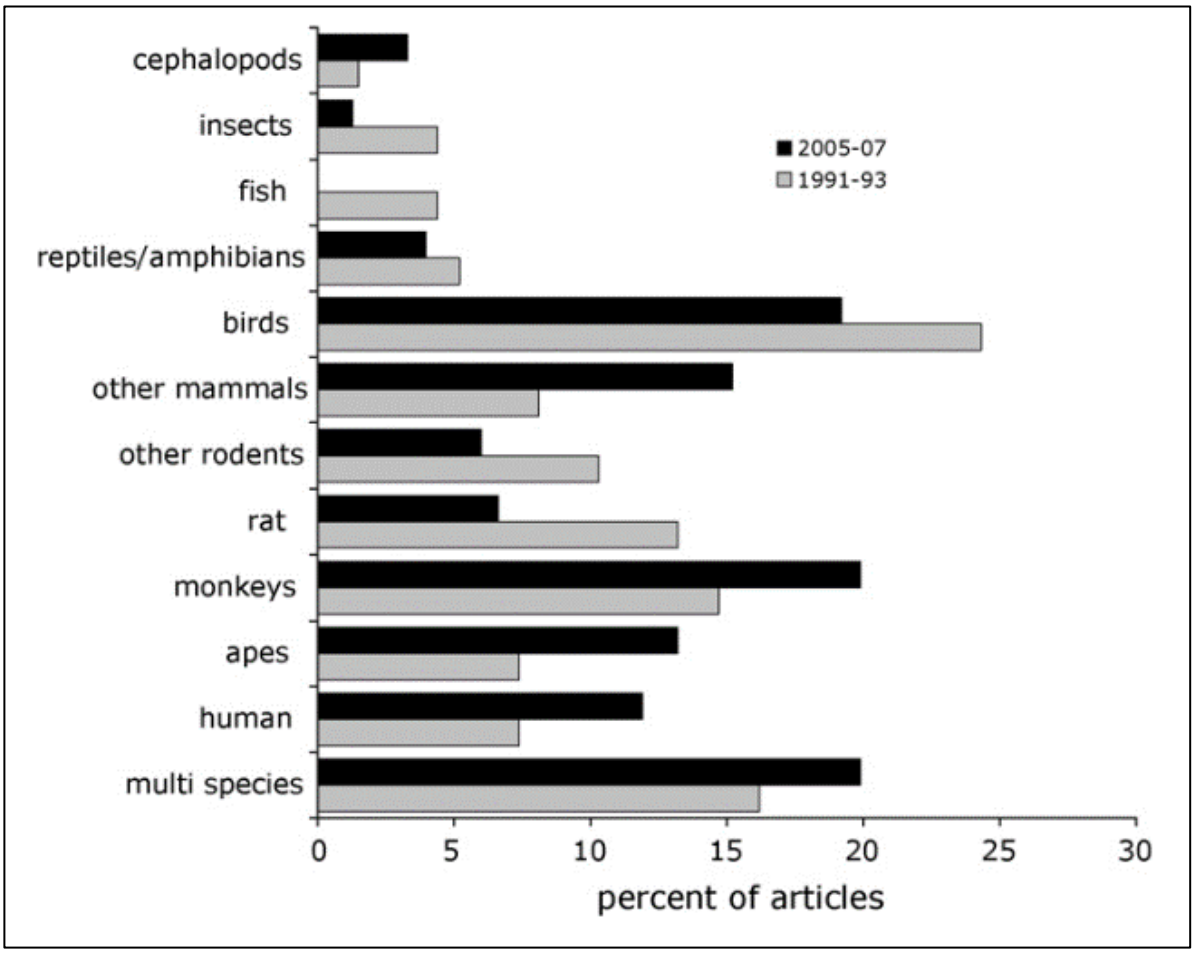


Figure 11 Figure from Shettleworth, 2009. Percentage of studies undertaken in different species and published in the period 1991-1993 and 2005-2007 (Data corresponding to studies published in the Journal of Comparative Psychology).

The range of topics studied has also increased since the field of comparative cognition has emerged. It involves for instance spatial and social cognition that are two dominant topics

(Beran et al., 2014) and also tool-use, memory, future planning, numerosity, communication, social learning, foraging, etc (e.g., Wasserman and Zentall, 2006; Shettleworth, 2010; Call et al., 2017; Zentall and Wasserman, 2012). While memory was a "hot" topic at the end of the 20th century and it still is today, its study has evolved through decades (Beran et al., 2014). It started primarily with stimulus-responses assessment for short and long-term memory (for instance with fear conditioning) and diversified with working and reference memory (e.g., Olten and Papas, 1979). Then, researchers tried to understand how animals navigate through the world, and whether they were able to remember information about spatial locations of object or event (Morris et al., 1984; Healy et al., 1999; Kelly and Gibson, 2007). The study of episodic cognition and future-oriented behaviour started around 20 years ago with the elaboration of the what-where-when paradigm and then diversified in a large range of species as described in more details in the section Episodic-Like Memory in Animals (e.g., Clayton and Dickinson, 1998; Griffiths et al., 1999; Correia et al., 2007; Cheke and Clayton, 2012; see Chapter 1 section A-1).

Over the last 20 years, a return to anthropocentric questioning was observed in this research field with a focus on topics such as theory of mind, mental time travel, and other renowned "uniquely human" capacities (Premack, 2007; Wynne, 2007; Penn et al., 2008 Shettleworth, 2010). These somewhat old-fashioned anthropocentric viewpoints of research seem to be still prevalent in actual research (Shettleworth, 2010; Eaton et al., 2018). For instance, studies investigate how animals understand the mental states of others as separate from their own mental state (theory of mind; Hare et al., 2001; Penn and Povinelli, 2007). There has also been a recent return to the question of self-awareness and self-recognition in comparative cognition with the mirror test (Pepperberg et al., 1995; Delfour and Marten, 2001; Plotnik et al., 2006; Roma et al., 2007; Prior et al., 2008).

A major issue in the comparative cognition field, is the methodology used to answer research questions. Because cognition is not directly observable, researchers need to rely on controlled tests allowing them to infer that a given behaviour is the reflection of a specific cognitive process (Wasserman and Zentall, 2006). This can lead to over-interpretation of findings and false-positive results. Recently, the problem of reliability and reproducibility of research was highlighted in the comparative cognition field (Farrar et al., 2020), revealing the necessity to always increase the number of new and replicated studies in one topic, and the number of species studied.

3. Choice of the species studied

Along with the need to increase the "comparative" in "comparative cognition", in my thesis I chose to investigate two very distinct species: the Eurasian jay (*Garrulus glandarius*), and the common cuttlefish (*Sepia officinalis*). Jays are the most renowned model of episodic-like memory, but some features of episodic cognition have not been studied yet. Cuttlefish, a mollusc cephalopod is the only invertebrate species for which episodic-like abilities have been shown (Jozet-Alves et al., 2013). However, much more data need to be collected in cuttlefish to fully integrate this species in a comparative and comprehensive approach of episodic cognition.

Complex cognition might have evolved as the result of multiple challenges associated with foraging for food (the Ecological Intelligence Hypothesis, Byrne, 1997; Janmaat et al., 2016), or as the result of complex social interactions (the Social/Cultural Intelligence Hypothesis, Schaik and Burkhart, 2011, Byrne, 2018), or both (Navarrete et al., 2016; Dunbar and Shultz, 2017). Another explanation for the evolution of intelligence in animal species also postulates that complex cognition evolved to cope with the challenges of predator-prey interactions (Byrne and Bates, 2007). Recently, complex cognition, such as episodic-like memory, has been described in distant related species such as corvids, mammals, and cephalopods (Emery and Clayton, 2004; Plotnik and Clayton, 2015; Amodio et al., 2019). Literature also supports evidence for shared neural circuits involved in memory in primates and birds (Güntürkün and Bugnyar, 2016). These behavioural and neurobiological data lead to think that complex cognition might have evolved convergently in these groups of species (e.g., in response to similar selective pressures, Emery and Clayton, 2004; for a review on the evolution of episodic memory see Allen and Fortin, 2013). Thus, investigating source-memory, in these very distinct species, could bring further knowledge on the evolution of episodic cognition.

Cephalopods were shown to share several complex cognitive abilities with vertebrates although they evolved under very distinct ecological pressures (they are not social animals, and have fast life histories with no parental care, Amodio et al., 2020): for instance problem solving and tool use (Amodio and Fiorito, 2013, Richter et al., 2016), complex defensive strategies (e.g., camouflage, Langridge et al., 2007; Hanlon and Messenger, 2018), or flexible behaviours in intraspecifics competition contexts (Brown et al., 2012). Modern cephalopods (i.e., octopods, squids, and cuttlefish) possess a central nervous system which resembles that of vertebrates by its relative size and complexity (e.g., it possesses functionally distinct brain structures such as

the vertical lobe involved in learning and memory for instance) supporting complex behaviours. As the hypotheses of the evolution of complex cognition were mostly based on mammal and bird behaviours (e.g., DeCasien et al., 2017; Ashton et al., 2018), studying cephalopod cognition would be extremely valuable to enrich our knowledge of the evolution of complex cognition.

II. Animal species studied in this PhD thesis

1. Eurasian jay (*Garrulus glandarius*)

Figure 12 Chinook who found a worm in the aviary.

Corvids

Corvids are passerine bird species including jays, crows, ravens, rooks, jackdaws, magpies, and nutcrackers (Ericson et al., 2005). They can adapt to various environments such as jungles, cities, mountains, and deserts (almost all types of environment except the polar ice caps), and are found in all continents except Antarctica (Clayton and Emery, 2005).

Corvids possess the largest brain related to body size of any other birds, and although their overall brain organization differ from those of mammals, some brain areas are considered functionally analogous (Clayton and Emery, 2015, Güntürkün and Bugnyar, 2016). For instance, the *nidopallium caudolaterale* seems to be analog of the primate prefrontal cortex (Güntürkün, 2005; Clayton and Emery, 2015, Figure 13). In addition, neuroanatomical studies

also showed that birds would possess primate-like number of cortical neurons in their forebrain (Olkowicz et al., 2016).

These neuroanatomical/functional data along with behavioural evidence of corvids' cognitive skills, argue in favour of corvid "intelligence", and corvids were recently nicknamed "feathered apes" (Emery, 2004; Clayton, 2012; Güntürkün et al., 2017). For instance, New Caledonian crows are able to select, use, and manufacture tools to solve problems (Chappell and Kacelnik, 2002; Rutledge and Hunt, 2004; Auersperg et al., 2011). Most corvids cache their food for later and can retrieve it weeks later. The most impressive record is the capacity of Clark's nutcrackers which can cache up to 30000 pine seeds and recover them up to 6 months later (Balda and Kamil, 1992).

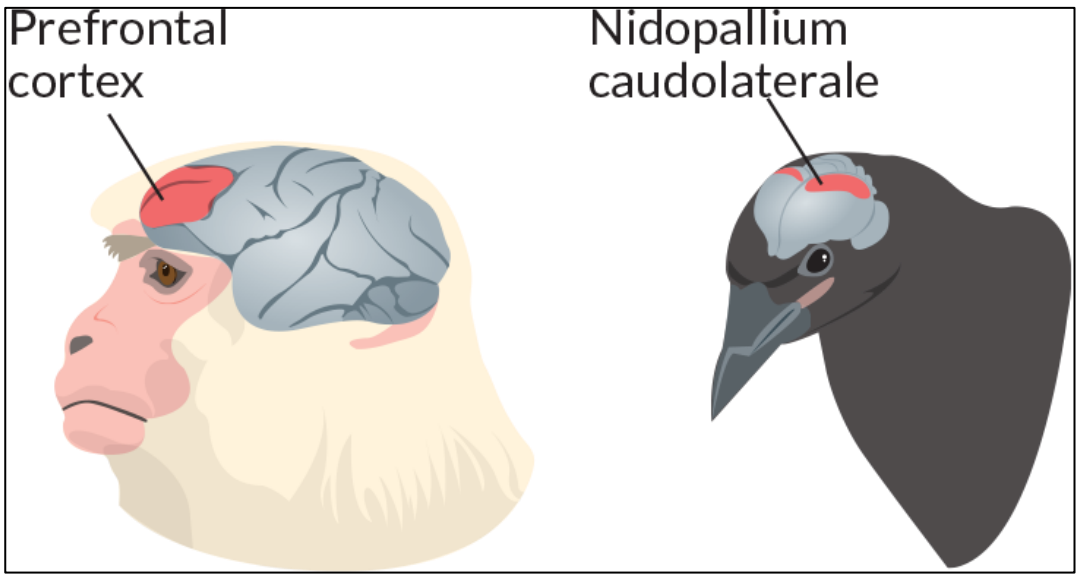


Figure 13 Illustration of the primate prefrontal cortex and the Nidopallium caudolaterale in corvids. Picture from Neider, 2016.

Eurasian jay

The Eurasian jays are easily recognizable by their beautiful plumage. Their head presents a white crest with black speckles, and their body have a light brown colour with a black tail. Most noticeable is their light blue and black streaked pattern on their wings (see Figure 12). They can weight from 200g to 300g and their body size is about 30 cm (Belabed et al., 2017).

They are part of the songbirds and they are renowned for their alarm calls that they use when they encounter a danger to warn their conspecifics. Their alarm calls can also prevent other species from the presence of predators, such as red squirrels for instance (Randler, 2006).

They are able to mimic the sounds they hear such as other birds' calls, human's or other animals' vocalizations (e.g., whistling) and even abiotic sound (e.g., water; lawn mowers, etc; Goodwin, 1951).

They are widely distributed throughout Europe and Asia in temperate environments. They are typically found in forests, parks, gardens, and orchards with dense foliage and plenty of trees where they can hide from predators (Goodwin, 1951). They can be hunted for instance by domestic cats, goshawks, sparrowhawks, tawny owls, and pine martens (Gurnell 1987; Glutz von Blotzheim and Bauer, 1993; Cramp, 1998).

They are omnivores and opportunistic, which mean that they can eat a large variety of food, and eat what they find. They can eat for instance acorns, fruits, grains, nuts, snails, worms, and other insects (Clayton et al., 1996). The Eurasian jays cache their food (mostly unperishable food; Goodwin, 1956) mostly in autumn and retrieve it throughout the year sometimes after months (Goodwin, 1951, 1956; Bossema 1979; Brodin, 2005; de Kort and Clayton, 2006; Shaw and Clayton, 2012; Shaw et al., 2013; Legg and Clayton, 2014; Shaw and Clayton, 2014).

Contrary to the rooks (*Corvus frugilegus*) and jackdaws (*Coloeus monedula*) that are highly social species, Eurasian jays are highly territorial and solitary. They only gather in the breeding season when they pair up (Goodwin, 1951; 1956). Eurasian jays are monogamous. They breed once a year during spring. At the beginning of spring (March-April), birds pair up their mate, and start their courtship behaviour. As part of the courtship, males and females (but mostly males) can share their food (e.g., Goodwin, 1951; Ostojic et al., 2016). Both parents participate to the building of the nest, and the females start to lay the eggs around the end of March. The parents provide food and care to the hatchlings until they reach two months old. Eurasian jays can live up to 16 years.

a. Sensorial systems
    i. Vision

Vision in humans is mainly binocular: our eyes are situated next to each other, closely, and focus on the same visual field (a visual field is a three-dimensional space within which the eyes can receive visual information; Martin and Osorio, 2008). On the contrary, vision in birds is mainly monocular. In most bird species, the eyes are on either side of the head and perceive different visual fields overlapping frontally to various extents depending on the species considered (Martin and Osorio, 2008). In scrub jays, the binocular visual field at rest is around 35°, while each monocular visual field is around 145° (Fernández-Juricic et al., 2010).

Colour vision is highly useful for a bird in the wild, for instance to detect food and predators and for choosing between partners (Bennett and Cuthill, 1994; Cuthill et al., 1999; Kemp et al., 2015). Birds seem to possess some of the most advanced colour vision abilities amongst other animals (Kelber and Jacobs, 2016; for a recent review see Kelber, 2019). Indeed, they possess a tetrachromatic vision (i.e., they possess four types of light receptors with different spectral sensitivities, allowing to perceive colour nuances; Kelber, 2019), where humans possess a trichromatic colour vision, and most mammals a dichromatic colour vision (Osorio, 2019; Kelber, 2019).

Bird's colour vision was experimentally studied in various birds including passerine birds showing for instance that zebra finch (*Taeniopygia guttata*) can discriminate colours (Lind, 2016), and are able to categorize them (Caves et al., 2018). Eurasian jays were also shown to be able to use colour cues to discriminate between apparatuses (Cheke et al., 2011). In laboratory experiments, corvids could detect shapes and black and white and coloured pictures (e.g., crows, Veit and Neider, 2013; Bogale and Sugita, 2014; Vonk, 2015).

ii. Olfaction

Birds seem to possess an olfactory system similar to that of other vertebrate species (Avilès and Amo, 2017). Experiments have shown that they are able to respond to chemical cues when foraging (e.g., *Procellariiform seabirds,* Nevitt et al., 1995; *Parus major,* Amo et al., 2013), orienting themselves in the environment (e.g., Wallraff, 2004; Nevitt and Bonadonna 2005; Gagliardo, 2013), avoiding predators (e.g., *Cyanistes caeruleus*, Amo et al., 2008), and during social interactions context (e.g., Caro and Balthazart, 2010).

Although passerines possess small olfactory bulbs (Buitron and Nuechterlein, 1985), studies showed that they are able to rely on olfactory cues in various contexts. For instance, ravens (*Corvus corax*) can detect food buried in gravels (Harriman and Berger, 1986). Magpies (*Pica pica*) are also able to locate food caches using olfactory cues (Buitron and Nuechterlein, 1985; Molina-Morales et al., 2020). Carrion crows (*Corvus corone corone*) respond to olfactory cues of conspecifics (Wascher et al., 2015).

iii. Audition

Passerines strongly rely on their sense of hearing to communicate with conspecifics in social and sexual contexts as well as in assessment of the risk of predation (Gleich and Manley, 2000). However, passerines do not have the best hearing abilities of all bird species. Although

they can hear high frequency sounds (i.e., high tones) easily, they are less accurate than non-song birds with low frequency sounds (i.e., low tones; Dooling et al., 2000). Nevertheless, a study showed that hooded crows (*Corvus corone cornix*) possess good low frequency sound detection compared to other passerines (Jensen and Klokker, 2005). Jays (*Aphelocoma californica*) can use auditory information when foraging (Stulp et al., 2009).

b. Cognitive abilities

Corvids are often presented as the most intelligent birds called "feathered apes" (Emery and Clayton, 2004). Indeed, although their common ancestor lived over 300 million years ago, and although their brain presents significant differences, primates and corvids seem to present similar cognitive abilities (e.g., tool use; learning and memory; sociocognitive abilities, etc; for a recent review see Baciadonna et al., 2020).

i. Episodic-like memory and prospective memory

In their original study, Clayton and Dickinson (1998, 1999) showed that jays (*Aphelocoma californica*) remembered what type of food they cached (i.e., wax worms, peanuts), where (i.e., the location in the tray) and how long ago (i.e., after a 4-hour or 124-hour delay).

The **content** of the what-where-when memory formed an integrated structure in the jays' memory (i.e., when animal remembers one aspect of the event, the other aspects will be automatically retrieved, Clayton et al., 2001b). This study confirmed the second criteria of episodic-like memory in jays (i.e., **structure**, the capacity to form an integrated representation of what-where-when).

Another study also revealed that this integrated representation could be used flexibly across different contexts (Clayton et al., 2003b). In this study, authors manipulated the perishability of the food: jays experienced that the perishable food degraded faster than expected. Results showed that jays searched preferentially for the non-perishable food to recache it in the original tray. This study validated the third behavioural criteria of episodic-like memory in jays (i.e., **flexibility**), showing that they were able to update their knowledge about the time of degradation of the different type of foods (Clayton et al., 2003b). Furthermore, the jays' performance in these experiments could not be explained by direct forgetting (de Kort et al., 2005).

Finally, scrub-jays were able to use past experiences to spontaneously plan for future events (Emery and Clayton, 2001; Raby et al., 2007) and in ways that clearly demonstrated that the birds were acting for future motivational needs not current ones (Correia et al., 2007; Cheke and Clayton, 2012). In the study of Raby and collaborators (2007), during several days in the morning, the jays were either invited to enter either in a "breakfast" compartment or to enter in a "no-breakfast" compartment. In the breakfast compartment, jays were given powered pine nuts to eat. In the no-breakfast compartment, no food was available. One evening, jays had the opportunity to cache pine nuts in the two previously described compartments. Results showed that jays significantly cached more pine nuts in the "no-breakfast" compartment than in the "breakfast" one, showing that they are anticipating their future hunger the next morning. In a subsequent experiment, Eurasian jays were also shown to be able to overcome their current needs to cache food that they will want to eat in the future (Cheke and Clayton, 2012).

ii. Tool use and causal reasoning

Corvids are known for their capacities to use and manufacture and innovate. These capacities have been considered as abilities demonstrating causal reasoning and flexibility (e.g., *Garrulus glandariu*s, Cheke et al., 2011; Davidson et al., 2017; *Corvus moneduloides*, Jacobs et al., 2016; *Corvus corax*, Kabadayi and Osvath, 2017; review: Seed and Byrne, 2010). For instance, it has been shown that Eurasian jays are able to use a stone to retrieve worms that were unattainable in a glass tube (Amodio et al., 2019). In this study, the jays had the opportunity to choose an appropriate size stone and drop it in the tube which caused an internal platform to collapse and food to fall out.

iii. Sociocognitive abilities

Corvids hide food that they will consume in the future. However, this is at risk of being pilfered by a conspecific (Dally et al., 2006), and it has been evidenced that jays take into account the presence or the absence of conspecifics when they are caching food (Emery and Clayton, 2001). For instance, Eurasian jays can use many cache-protection strategies such as caching their food when they are out of sight, or at distance from conspecifics, and avoiding caching in noisy substrate (i.e., a substrate that makes noise when the jays cache food, such as a rocky substrate for instance), especially when observed by a potential pilferer (Shaw and Clayton, 2013; Legg and Clayton, 2014; Legg et al., 2016). This ability to flexibly use caching-protection strategies according to the presence or the absence of a potential pilferer has been discussed as the capacity to attribute knowledge to a conspecific as for instance what they can

see or hear from the caching event (Emery and Clayton, 2004; Dally et al., 2006; Clayton et al., 2007; Emery and Clayton, 2009; Bugnyar et al., 2016; Keefner, 2016). The ability of Eurasian jays to attribute knowledge to others has also been evidenced in studies investigating food-sharing (Ostojic et al., 2013; Ostojic et al., 2014). In these studies, male Eurasian jays were feeding females with the food they were not pre-fed with, showing that males take into account the satiated state of the females and flexibly orient their food-sharing decisions (Ostojic et al., 2016).

2. The common cuttlefish (*Sepia officinalis*)

Figure 14 Juvenile cuttlefish imitating the rock next to it and detecting a prey in its tank.

Cephalopods are part of the molluscs whose evolution diverged from that of vertebrates around 500 million years ago. There are around 700 different species of cephalopods, divided in two sub-classes. The Nautiloidea have the particularity to possess an external shell and two pairs of gills (Jereb and Roper, 2005). The Coleoidea are composed of the octopods possessing eight arms (e.g *Octopus vulgaris*), and the squids and cuttlefishes (e.g., *Sepia officinalis,* Figure 14) possessing two very long tentacles in addition to their eight arms.

Common cuttlefish can be found in the English Channel, the Atlantic Ocean, and in the Mediterranean Sea: from the South of Norway and the North of England to the North-West coasts of Africa (Guerra, 2006, Figure 15). Cuttlefish are nectobenthic, they live on the bottom of the sea and spend most of their time either on the substrate or buried in the sand. They can

be encountered by the coastlines at around 2 or 3 meters' depth but also further when the water depth reaches 100 to 200 meters (Guerra, 2006). Given the variety of coasts where they can be found, common cuttlefish can live in a wide range of water temperatures: from 10° to 30°. The colder the water, the more inactive the cuttlefish become, and under 10° they rapidly die as they do not eat anymore (Martinez et al., 2000).

Cuttlefish live approximately two years. They have the particularity to migrate seasonally between shallow and deep waters. These migrations are most likely influenced by water cooling and light reduction in winter (Boletzky, 1983; Boucaud-Camou and Boismery, 1991). In the English Channel, cuttlefish show a biannual life cycle where they migrate from the coasts in late autumn to the hibernation zone situated in deeper water at the central axis of the Channel (Guerra, 2006), where they stay until the end of winter. In spring, they come back to the coasts.

The reproductive season starts around February and ends around July (Dunn 1999; Royer, 2002; Wang et al., 2003). Cuttlefish lay their eggs on living or non-living structures such as tube worms, seaweed, cables, or nets. Neither the eggs nor the young hatched cuttlefish receive parental care as females die shortly after spawning. Newly hatched cuttlefish present the same behavioural repertoire than adults, (although they need to perfect it) and can immediately start feeding on small preys.

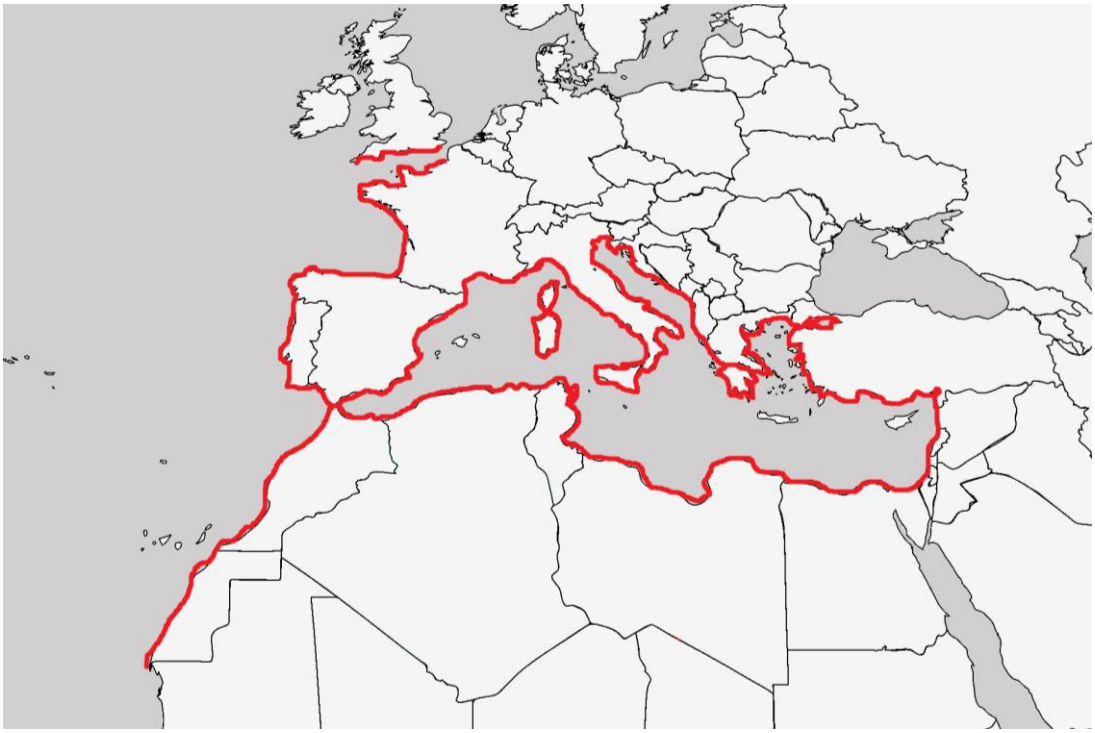


Figure 15 Dispersion of cuttlefish Sepia officinalis in North-West Atlantic and Mediterranean Sea.

Cuttlefish eat crustaceans (e.g., shrimps, prawns, crabs), fishes (e.g., gobies, eels, whiting, wrasses), and molluscs (e.g., cannibalism has been described; Castro and Guerra, 1990; Pinczon du Sel et al., 2000; Guerra, 2006; Figure 16). In the wild, they only hunt live preys although they can be taught to eat dead preys or non-living food (e.g., surimi). Their diet has been described as opportunistic (Guerra, 2006), which means that they eat what they find in their environment.

Figure 16 Juvenile cuttlefish catching a shrimp by ejecting its tentacles (pictures taken by Manon Peyrafort).

The body of cuttlefish is divided in two parts (Figure 17): the *visceropallium,* composed of the mantle, the fins, the internal shell (i.e., the cuttlebone or sepion which is calcareous and allows the cuttlefish to adjust its buoyancy; Nixon and Young, 2003), and organs (e.g., the respiratory, digestive and reproductive organs, the ink sac, etc.). The *cephalopodium* houses the brain of the cuttlefish, holds two big eyes, the funnel, the beak and eight arms attached around the mouth, and two retractable tentacles. At rest, these two long tentacles are folded in pouches situated below the eyes (Mangold et al., 1989).

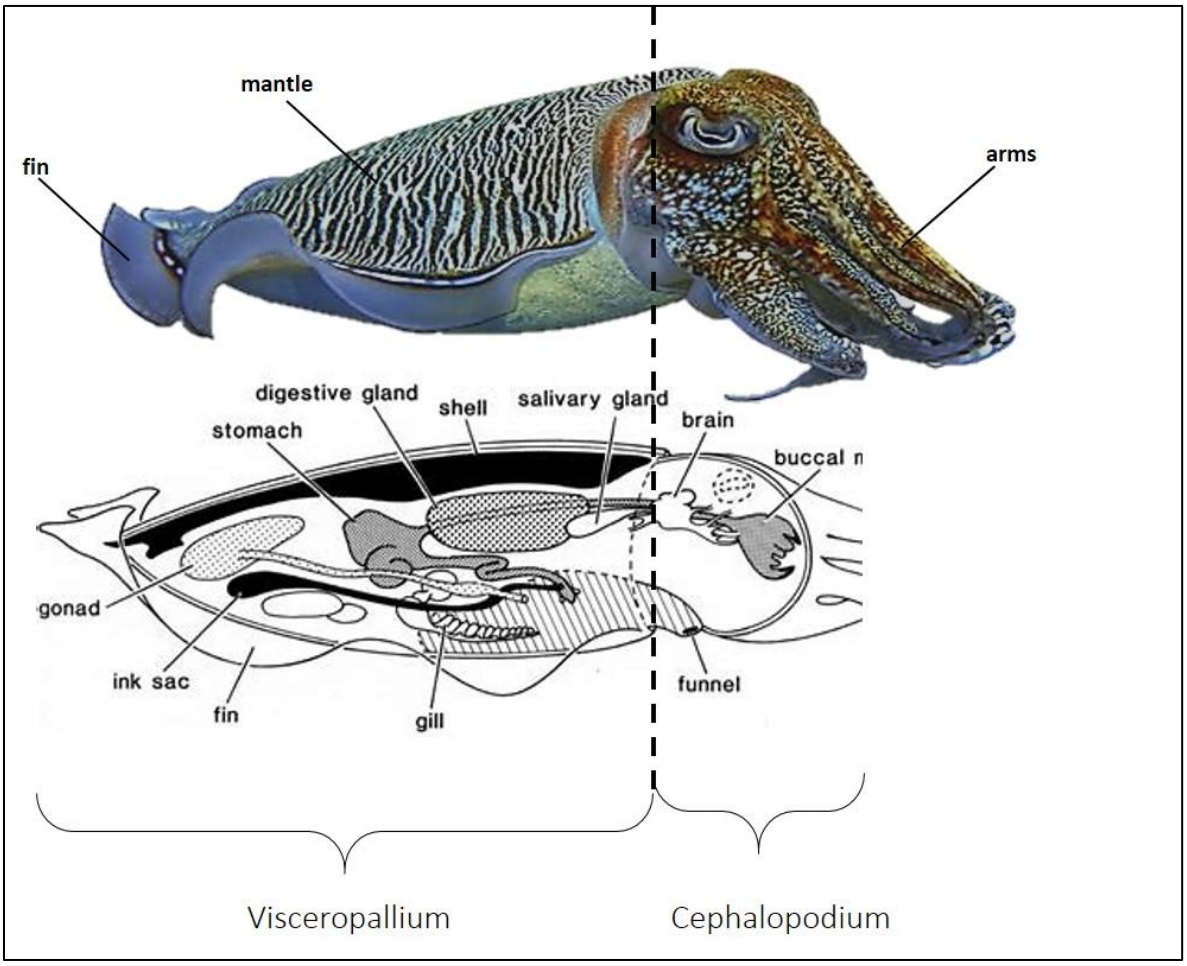


Figure 17 Cuttlefish Sepia officinalis anatomy. Picture adapted from Boletzky and Villanueva, 2014.

a. Sensory systems

Cuttlefish perceive visual, chemical, and tactile information. Studies also showed that they can perceive vibrations from their environment (e.g., Samson et al., 2014; Wilson et al., 2018). However, in the context of this thesis, I will only focus here on visual and olfactory systems.

i. Vision

Cuttlefish are renowned for their highly developed visual system, whose crucial role was evidenced during predation (e.g., Messenger, 1968), camouflage (e.g., Hanlon and Messenger, 1988; Barbosa et al., 2008b; Zylinski et al., 2012), navigation (e.g., Cartron et al., 2012), or interspecific communication (e.g., Adamo and Hanlon, 1996). The eyes situated on each side of the head, can converge through extraocular muscles (Budelmann and Young, 1993). When the eyes are laterally positioned, their visual fields almost equal 360°, and when the eyes converge, their visual field is reduced to 75° (Messenger, 1968). Although cuttlefish cannot see

colours, they are sensitive to the plane of polarization of light (Shashar et al., 2002). This ability makes them able to increase perception of silvery fish whose scales reflect light (Shashar et al., 2000).

The visual system of cuttlefish is efficient before hatching. Embryonic visual experience can affect post-hatching feeding and defensive behaviours (for a review see Darmaillacq et al., 2017). For instance, cuttlefish food preference can be modified by embryonic exposure to a specific prey (e.g., Darmaillacq et al., 2008; Guibé et al., 2010; 2012). Pre-hatching visual stimulation can also affect later shelter and background preferences (Guibé and Dickel, 2011; Lee et al., 2012). These experiments show cuttlefish ability to perceive contrast and brightness before hatching.

Cuttlefish highly developed visual system allows them to camouflage on different substrates that vary in textures (e.g., Kelman et al., 2007; Chiao et al., 2009), patterns (e.g., Hanlon and Messenger, 1988, Figure 18), and contrasts (e.g., Marshall and Messenger, 1996; Mäthger et al., 2006; Hanlon et al., 2013). Their camouflage abilities are mostly visually driven (e.g., Barbosa et al., 2007, 2008a,b; Chiao et al., 2005, 2007; Mäthger et al., 2007; Reiter and Laurent, 2020). It has been shown that cuttlefish can detect horizontal and vertical aspects of the visual background which can play a role in their camouflage (Barbosa et al., 2008a). Laboratory experiments also showed that cuttlefish can detect proximal and distal (i.e., located outside water) visual cues such as white PVC squares with black shapes on them and use them as part of various learning (e.g., Alves et al., 2007; Jozet-Alves et al., 2013; Scatà et al., 2016).

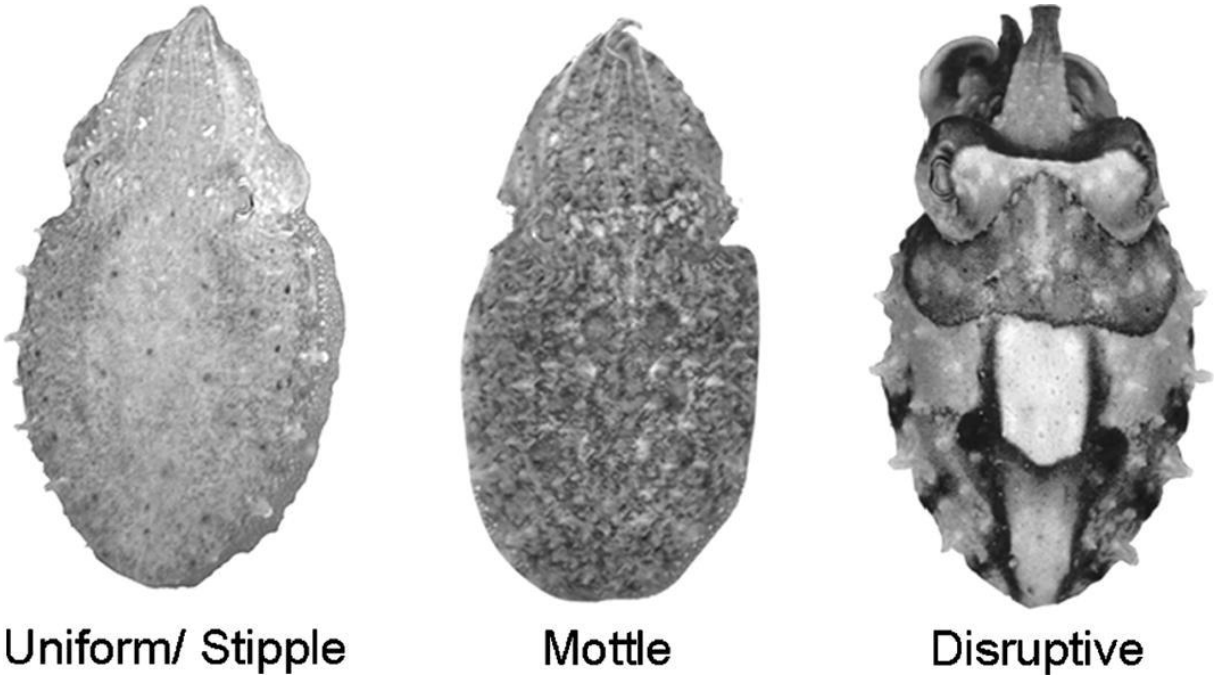


Figure 18 Different types of camouflage patterns expressed by the cuttlefish Sepia officinalis. Picture from Barbosa et al., 2008b.

ii. Olfaction

While they are thought to rely mostly on vision, the role of chemoreception in cuttlefish has been evidenced (e.g., Hanlon and Shashar, 2003). It has been showed that cuttlefish possess olfactory cells involved in distance chemoreception situated under the skin behind the eyes (Tompsett 1939; Wildenburg 1991). Chemoreceptors have also been described on the suckers of the arms and tentacles as well as in the region surrounding the mouth (Sundermann, 1983; Nixon and Mangold, 1998; Figure 19).

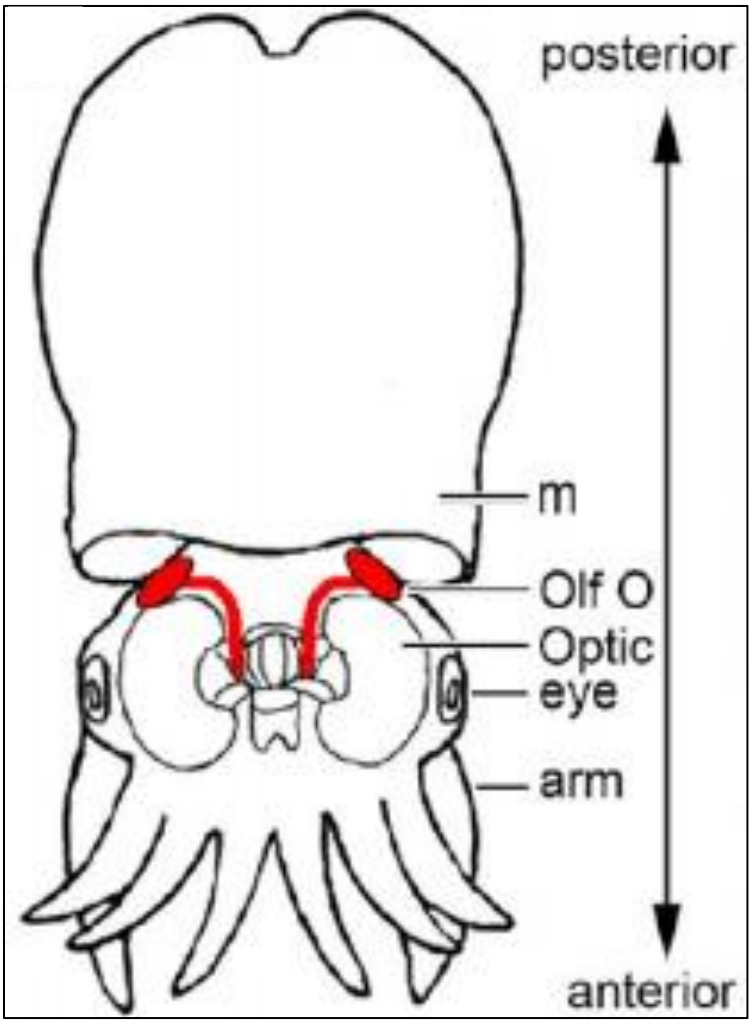


Figure 19 Emplacement of the olfactory organs (Olf O) in red in the picture. Picture from Scaros et al., 2018.

Behavioural evidence for distance chemoreception comes from studies showing that cuttlefish are able to detect the odour of food, predators and conspecifics (Budelmann, 1997; Boal and Marsh, 1998; Boal and Golden, 1999). For instance, they can choose the most sexually available partner based on chemical cues (Boal, 1996, 1997), and sexually mature cuttlefish can detect odours from other cuttlefish eggs (Boal et al., 2010). More recently, studies showed that cuttlefish embryos responded to predator odour (Romagny et al., 2012, Mezrai et al., 2019), and that food preferences and behavioural asymmetries are altered in newly hatched cuttlefish after embryonic exposure to prey odours (Guibé et al., 2010; Jozet-Alves and Hébert, 2013), showing that this ability is functional before hatching (see O'Brien et al., 2017 for a review on the behavioural development in cuttlefish *Sepia officinalis*).

b. Cognitive abilities

Learning abilities of coleoid cephalopods (i.e., cuttlefish, octopods, and squids) have been investigated since decades (e.g., Messenger, 1973; for recent reviews see Dickel et al., 2013;

Marini et al., 2016). Cuttlefish abilities have been evidenced for various types of learning such as habituation (e.g., Samson et al., 2014); classical and operant conditioning (e.g., Purdy et al., 1999); discrimination learning (e.g., Hvorecny et al., 2007); and generalization (e.g., Guibé et al., 2012).

i. Associative learning

Cuttlefish can perform associative learning tasks, mostly evidenced in the "prawn-in-the-tube" procedure (Messenger, 1973; Agin et al., 2006; Purdy et al., 2006; Cartron et al., 2013). In these studies, prawns are put in a glass tube placed in the tank of the cuttlefish. Cuttlefish try to catch the preys that are unreachable, and progressively learn to stop attacking them. Researchers showed that this behaviour was not due to motor fatigue (Messenger, 1973), pain (Agin et al., 1998; Cartron et al., 2013), and that the decrease of catching attempts is unlikely due to habituation (Purdy et al., 2006; Agin et al., 2006).

Associative learning was also evidenced in classical conditioning in cuttlefish (e.g., Purdy et al., 1999; Cole and Adamo, 2005). For instance, cuttlefish learnt that the presentation of a more or less bright sphere was associated with the distribution of food and started attacking the rewarded stimulus even before the food was delivered (Cole and Adamo, 2005).

ii. Spatial learning

Researchers demonstrated that cuttlefish can also use different strategies in spatial learning tasks, similarly to vertebrates (Karson et al., 2003; Alves et al., 2006, 2007; Jozet-Alves et al., 2008; Cartron et al., 2012; Scatà et al., 2016). For instance, in the study of Alves and collaborators (2007), cuttlefish had the opportunity to reach a comfy compartment (with shadow and sand). To reach this compartment, cuttlefish could either rely on their own motor sequence (turn left or right) or on visual cues (striped and spotted PVC panels) or even visual distal cues. Authors showed that individuals relied on different strategies depending on the availability and salience of the visual cues (Alves et al., 2007), and on the sex of tested individuals (Jozet-Alves et al., 2008). More recently, it has been showed that cuttlefish use the vertical space during their daily paths if it is more efficient than moving next to the bottom (Scàta et al., 2017), and that they can recall separately the vertical and horizontal components of a previously learned two-dimensional target (in a 2D vertical plane; Scatà et al., 2016).

iii. Social learning

Social learning in cuttlefish has shown contradictory results. For instance, Boal and collaborators (2000) showed that cuttlefish were not able to learn predation technics to catch a crab by observing conspecifics. Evidence for the lack of social learning in cuttlefish was relayed by Huang and Chiao (2013), who provided unclear results on cuttlefish ability to avoid danger by observing others. However, these results were disputed by recent studies showing that cuttlefish can learn from others in the wild (Yasumoro et al., 2015) and in experimental conditions (Sampaio et al., 2020). In this last study, juvenile cuttlefish learnt to avoid attacking a glass tube with a shrimp inside (i.e., prawn-in-the-tube procedure) by observing a conspecific performing the task.

iv. Episodic-like memory

As mentioned in "What-Where-When (In Terms of How Long Ago)", it has been evidenced that cuttlefish possess episodic-like memory abilities (Jozet-Alves et al., 2013).

In this experiment, cuttlefish were first trained to go next to a visual cue to get food. Then, they were trained to learn that: when their favourite food (i.e., shrimp) is eaten, they need to wait three hours until this type of food item get replenished, while their non-preferred food (i.e., crab) was always available. During the episodic-like memory task, each cuttlefish was tested once per day (i.e., one trial per day), each trial was constituted by two phases with either a short or a long delay separating them (Figure 20). During the first phase, two identical visual cues were placed in the tank in two different locations. When cuttlefish went randomly close to one of these visual cues, a shrimp and a crab were placed in the tank, one in front of each visual cue. The cuttlefish was allowed to capture one of the two preys. Then, the two visual cues were removed from the tank.

During the second phase, the two visual cues were placed back in the tank at the same locations (than at the first phase of the same day) either after 1 hour or after 3 hours (randomized across subjects and across days). After the 1-hour delay, cuttlefish were rewarded only if they went close to the visual cue located where the non-preferred prey was seen at phase 1 (i.e., only crab was available). After the 3-hours delay, cuttlefish were rewarded with the corresponding prey when they went close to one of the two visual cues (i.e., both preys available).

Results showed that cuttlefish revisited more the location associated to the non-preferred prey after the short delay, whereas they revisited more the location associated to their preferred prey after the long delay. These results showed that cuttlefish were able to remember what type of prey was available, where and when (how long ago the prey was encountered).

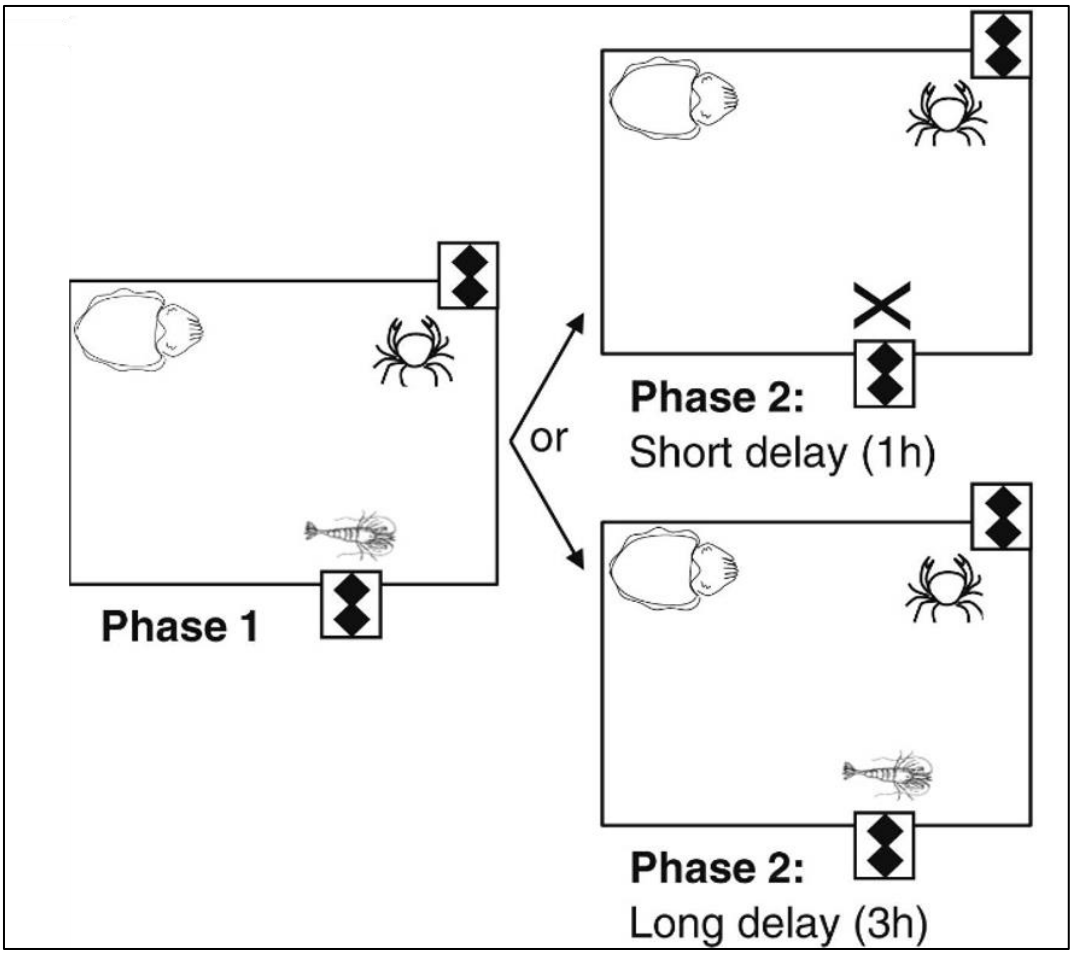


Figure 20 Design of the episodic-like memory study in cuttlefish. Picture from Jozet-Alves et al., 2013.

v. Flexibility in intraspecific interactions

Cuttlefish display amazing flexible behaviours during intraspecific interactions in the wild. For instance, male cuttlefish (*Sepia apama*) can mimic females (i.e., colour and posture) to approach an already paired female in front of the consort male (Hanlon et al., 2005). This surprising behaviour seems to be observed as a strategy for little males to mate with females in the presence of other males. In *Sepia plangon*, it has been shown that males show a courtship colouration towards a receptive female on one side, and show a camouflage imitating a female towards a rival male on the other side of the body (Brown et al., 2012). Flexible behaviour was also observed in *Sepia apama* during agonistic behaviours, where males adjust their fighting strategy in accordance to the size and fighting ability of their rival (Schnell et al., 2015).

vi. Neural substrates of learning and memory

Cuttlefish possess a centralized nervous system (for a review see Agin et al., 2006, see also Nixon and Young, 2003, Figure 21a). Their brain is situated in-between their eyes, clustered around the anterior part of the oesophagus, and is protected by a cartilage (Tompsett 1939;

Bullock, 1965; Budelmann, 1995). It is composed of two big optic lobes and a central mass. The central mass comprises a supra- and a suboesophageal parts connected by perioesophageal lobes. The brain is subdivided in numerous interconnected lobes. Most lobes are composed of a neuropil (network of fibres) surrounded by a cortex (cell layers). Cuttlefish brain presents an impressively high number of neurons (100-200 million neurons, Budelman, 1994) which participate to the complexity of their neural system.

The sub- and periesophageal lobes are classified as lower and intermediate motor centres, involved for instance in the swimming control, escape behaviours, ink ejection and movements of the arms and tentacles (see Nixon and Young, 2003). The supraesophageal mass comprises higher motor centres, secondary sensory centres, and finally the vertical lobe complex located in the dorsal part (Boycott 1961; Borrelli and Fiorito, 2008; Marini et al., 2016). Several studies have shown that the dorsal part of the supraesophageal mass (i.e the vertical lobe system) is specifically involved in learning and memory (Sanders, 1975; Agin et al., 2006; Shomrat et al., 2011; 2015; Hochner and Shomrat, 2013). As my PhD thesis focuses on memory, I will present this part of the brain in more details.

The vertical lobe complex

The vertical lobe complex is constituted of several lobes: the superior frontal, the subvertical, and the vertical lobes (Young 1965; Figure 21b). It has been showed that these lobes are involved in acquisition and in retention processes (e.g., Messenger, 1977; Dickel et al., 2001; Agin et al., 2001).

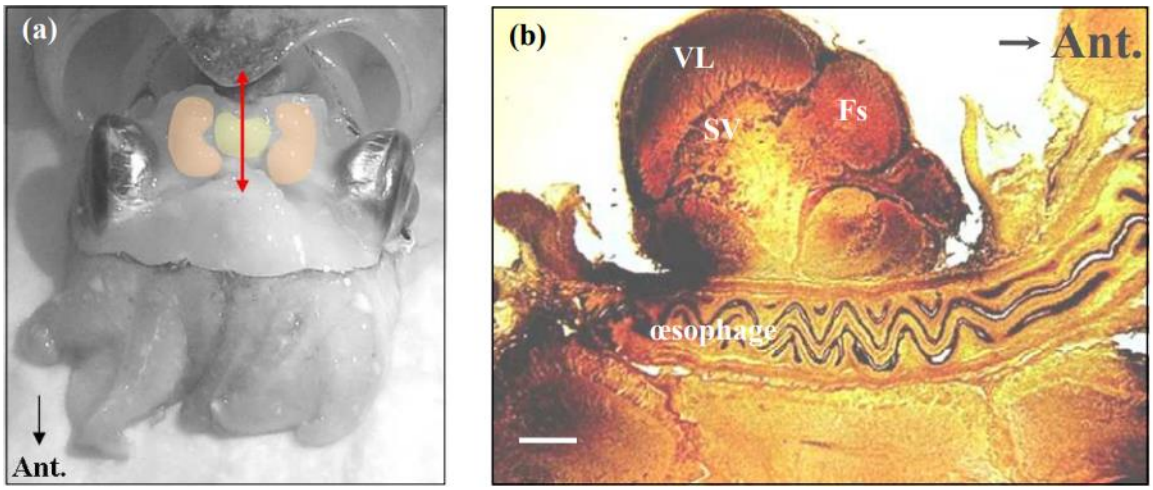


Figure 21 Central nervous system of the cuttlefish, Sepia officinalis. (a) Picture of the central nervous system (in yellow) after opening the brain's cartilage. The optic lobes are represented in orange. The red arrow indicates the cutting plane of the brain shown in (b). (b) Sagittal section of the central nervous system with the vertical lobe complex in the dorsal part. VL= Vertical lobe, Fs= Superior frontal lobe; SV= Subvertical lobe. Scale = 500 µm. Picture from Jozet-Alves, 2008.

The vertical lobe is called “silent area” because electric stimulation of this lobe does not elicit any motor responses in the cuttlefish (Boycott, 1961; Shomrat et al., 2015). In juveniles, studies found a correlation between the development of the vertical and the superior frontal lobes and the development of long-term memory (Dickel et al., 2001). In this study, cuttlefish of different ages (from 8 days-old to 90 days-old) were presented with the prawn-in-the-tube procedure. Results showed that newly hatched cuttlefish (i.e., 8 days-old) were less efficient than older cuttlefish in training and retention after a 30-minute delay, showing that memory abilities develop until 30 days old (Dickel et al., 1998; Dickel et al., 2001). Between 30 and 90 days old, when cuttlefish were asked to perform the task after a 24hours delay, they showed significant enhancement of performance, showing an increase of long-term retention at these ages. These behavioural results were correlated with volume measurement of the vertical and the superior frontal lobe, growing until 90 days of age.

In cuttlefish, two studies have evidenced the role of the vertical lobe in long-term memory using chirurgical ablation or electrolytic lesions. In the first study, the ablation of the vertical lobe impaired visual long-term learning (Sanders and Young, 1940). However, the ablation damaged the surrounding lobes and there was the need to confirm the specific implication of the vertical lobe in long-term acquisition and retention processes. In the other study, the authors applied electrolytic lesions in the ventral and the dorsal part of the vertical lobe. Cuttlefish performances in spatial maze revealed that ventral lesions impaired acquisition of a spatial task, while dorsal lesions impaired long-term retention of spatial learning (Graindorge et al., 2006). More recently, it has been shown that stimulation of the inputs from the superior frontal lobe leads to an activity-dependent long-term potentiation in the dorsal part of the vertical lobe (Shomrat et al., 2011).

One study showed the role of the superior frontal lobe in learning and memory processes. In this study, authors showed metabolic changes in neuronal cells of the superior frontal lobe after the prawn-in-the-tube learning which would be linked to the changes of neuronal activity during consolidation (Agin et al., 2001).

The vertical-subvertical lobe tracts have been evidenced to play a key role in short-term memory processes (Dickel et al., 1997). In this study, newly hatched cuttlefish were observed displaying predatory behaviour (i.e., pursuit of preys). This behaviour is linked to short-term memory as cuttlefish need to remember the characteristics of the prey when it disappears from their vision field. Authors found a positive correlation between the development of the vertical-

subvertical lobe tracts and the emergence of prey-pursuing behaviour in cuttlefish, suggesting their involvement in short-term memory processes. In senescent cuttlefish, the retention of the prawn-in-the-tube learning is negatively correlated with the presence of degenerating fibres in the vertical-subvertical tracts (Chichery and Chichery, 1992), confirming their role in learning and memory.

The optic lobes

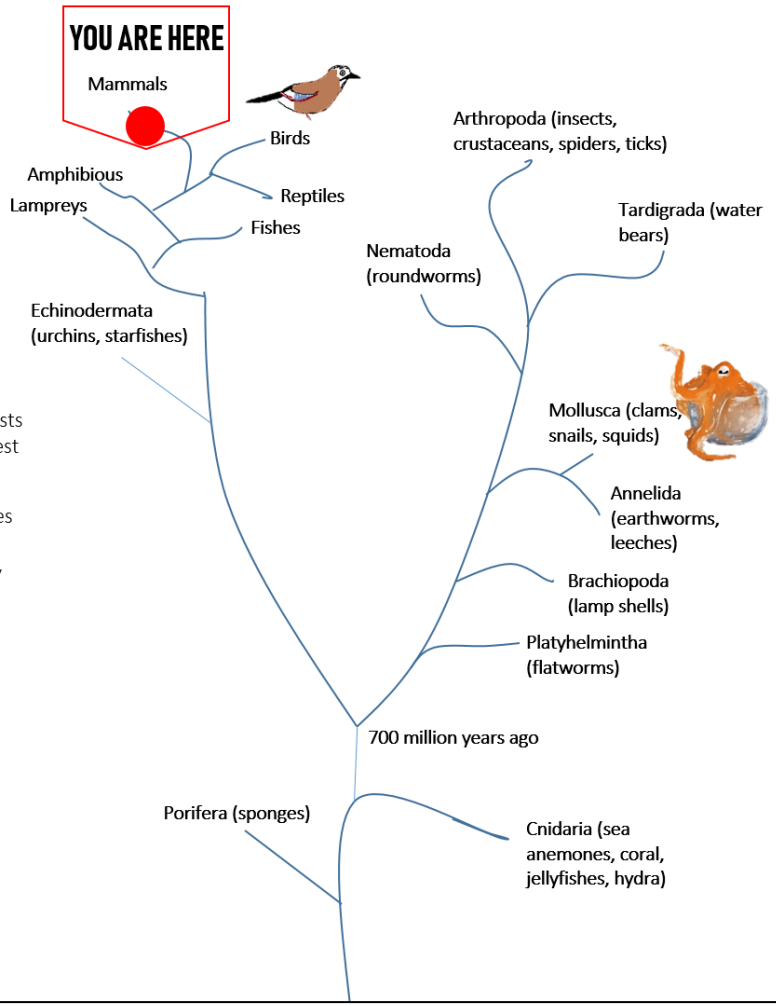
Within the central nervous system of the cuttlefish, the optic lobes are situated on each side of the brain, close to the eyes (Figure 21a). They are involved in higher-order visual information processing, in the control of motor actions (Boycott, 1961; Chichery and Chanelet, 1976, Liu et al., 2017), as well as in learning and memory (e.g., Williamson and Chrachri, 2004). For instance, an increase of acetylcholine (neurotransmitters involved in learning and memory) in the optic lobes 24hours after an associative learning procedure seem to argument in favour of the involvement of the optic lobes in long-term retention (Bellanger et al., 2003).

Summary outline of some of the ecological differences and the cognitive similarities between the Eurasian jays and the common cuttlefish.

Eurasian jay
Garrulus glandiarius

Common cuttlefish
Sepia officinalis

Common ancestor	300 million years ago	500 million years ago
Distribution	Dense foliage environment/ Europe and Asia in temperate environments	Sandy, muddy bottoms, close to the coasts and further (100-200m deep). North-West Atlantic and Mediterranean Sea
Diet	Omnivores	Molluscs, worms, crustaceans, little fishes
Reproduction	Once a year during the breeding season (Mars-July)	Once in life, reproduction February-July/ Laying eggs in spring
Parental care	Newly borns receive parental care until they reach two months old	No parental care
Defense	Alarm call / attack	Camouflage
Lifespan	16 years	2 years
Common cognitive abilities	Associative learning Episodic-like memory Flexible behaviour Sociocognitive strategies	Associative learning Episodic-like memory Flexible behaviour Sociocognitive strategies



CHAPTER

2

EXPLORATION OF SOURCE-MEMORY IN CUTTLEFISH AND JAYS

Article 1:
Billard, P., Clayton, N. S., & Jozet-Alves, C. (2020). Cuttlefish retrieve whether they smelt or saw a previously encountered item. *Scientific reports 10:5413. DOI: 10.1038/s41598-020-62335-x*

Article 2:
Billard, P., Jozet-Alves, C., Clayton, N. S. (in revision in Animal Behavior and Cognition) A new paradigm for assessing discriminative learning and incidental encoding of task-irrelevant contextual cue in Eurasian jays.

Introduction of Chapter 2

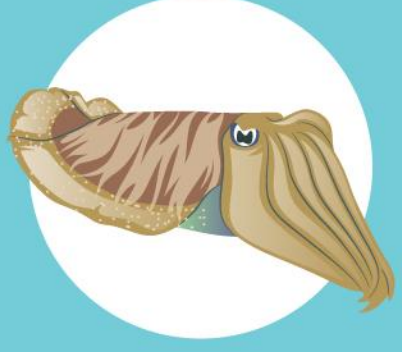
This chapter presents two different protocols to investigate source-memory in cuttlefish *(Sepia officinalis)* and jays *(Garrulus glandarius)*.

Article 1 / Part 1: Exploration of source-memory in cuttlefish:

This study is inspired from the item vs source experiment in humans. Cuttlefish have the opportunity to retrieve specific characteristics of an event (i.e. perceptual characteristics), in order to make a choice between two different sources during an unexpected test, by answering the question "Did I see or did I smell?". First, cuttlefish were presented with a source-discrimination task where they were trained to differentiate between visual and olfactory stimuli. In the unexpected source-memory test, they needed to remember the modality of presentation (i.e. visual or olfactory) of a previously encountered item (several hours before). We hypothesized that if cuttlefish are able to remember in which modality the item was previously encountered, while they have not been trained to do so, then it would indicate the involvement of source-memory processes.

Article 2 / Part 2: Exploration of source-memory in Eurasian jays:

In the second source-memory study, we investigated jay's ability to incidentally encode a contextual cue. Jays were first trained to solve a simple discrimination task. To perform this task, they had the opportunity to land on one of two perches, each one being associated with a different type of picture. Simultaneously, they were presented with a contextual cue (a visual shape fixed on the wall of the testing room) which was completely irrelevant to solve the discrimination task. In the source-memory test, jays were unexpectedly asked to retrieve which kind of picture was previously encountered in the presence of a contextual cue (information which was previously irrelevant to solve the task). We hypothesized that if jays were able to retrieve which picture was seen in which context, then it should be indicative of source-memory processes.



I. Exploration of source-memory in cuttlefish

Cuttlefish retrieve whether they smelt or saw a previously encountered item.

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DOI: 10.1038/s41598-020-62335-x

Abstract

According to the Source Monitoring Framework, the origin of a memory is remembered through the retrieval of specific features (*e.g.,* perceptive, sensitive, affective signals). In two source discrimination tasks, we studied the ability of cuttlefish to remember the modality in which an item had been presented several hours ago. In Experiment 1, cuttlefish were able to retrieve the modality of presentation of a crab (visual *vs* olfactory) sensed before 1h and 3hrs delays. In Experiment 2, cuttlefish were trained to retrieve the modality of the presentation of fish, shrimp, and crabs. After training, cuttlefish performed the task with another item never encountered before (e.g., mussel). The cuttlefish successfully passed transfer tests with and without a delay of 3hrs. This study is the first to show the ability to discriminate between two sensory modalities (*i.e.,* see *vs* smell) in an animal. Taken together, these results suggest that cuttlefish can retrieve perceptual features of a previous event, namely whether they had seen or smelled an item.

Keywords: Source-memory, Perception, Cognition, Cuttlefish, Cephalopods

Billard, P., Clayton, N. S., & Jozet-Alves, C. (2020). Cuttlefish retrieve whether they smelt or saw a previously encountered item. Scientific Reports 10:5413. DOI: 10.1038/s41598-020-62335-x

Introduction

Can you tell whether you *truly* enjoyed your last holiday? According to the Source-Monitoring Framework (SMF), answering such a question requires you to revisit your personal past and retrieve specific features belonging to your memories (*e.g.,* affective, perceptual and contextual features, Johnson et al., 1993). For instance, I can remember that I went to my parents' home town (contextual features), and that we spent evenings talking or playing music (perceptual features) in a joyful atmosphere (affective feature). To remember these specific details and moments, I travelled mentally back through my personal past and engaged in *episodic cognition processes,* projecting myself in space and time to re-live and re-experience the content of those personal memories, integrating the contextual, perceptual and affective features. Travelling mentally back into one's personal past is referred to as *episodic memory*, while retrieving specific features belonging to these episodic memories is a cognitive capacity involving *source-memory* processes. Source-memory is embedded into the episodic memory, and triggers semantic processes aiming at retrieving the origin of a memory and enabling to distinguish between two or more episodic memories. In humans, source-memory is mostly studied using item *versus* source-memory discrimination task. As the memory of the source relies on the recall of specific characteristics of a prior situation, participants are asked to retrieve the features of the context in which items were previously encountered. In such studies, participants have to recall the items they encountered earlier in opposition to new items (item memory), and then retrieve the context in which they were presented (*e.g.,* whether the target items were read or mentally imagined, Davachi et al., 2003; their spatial location, Slotnick et al., 2003; the list to which they belonged, Trott et al., 1997; the colour of the item, Cycowicz, 2011, etc; source-memory). Only few studies have focussed on source-memory in non-human animals. One single experiment mimicked the item *versus* source procedure in monkeys (Basile and Hampton, 2017). Rhesus monkeys learnt to respond differently to two images (*i.e.,* the first needed to be simply touched and the second one should be classified as bird, fish, flower, or human). At test, four images were presented (the two previously seen images and two distractors) and half of the monkeys needed to retrieve the image previously simply touched, and half of the monkeys needed to retrieve the image previously classified. Monkeys showed their ability to discriminate between the two sources when test was presented after a short delay, but they made source-memory mistakes when tested after a long delay, while still avoiding distractors (item memory preserved). Crystal and colleagues (2013), studied rat's ability to discriminate between self- or externally-generated information. This study focused on another

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type of source-memory, called reality monitoring (i.e., did I learn this information myself, or did I learn it from someone else? Johnson et al., 1993). Apart from monkeys and rats, source-memory has not been investigated in other species, and it is not known to what degree the ability to remember the source of an event is a shared capacity between species or if it is a specific cognitive feature of mammals.

Cuttlefish (*Sepia officinalis*) belong to the group of coleoid cephalopod molluscs. They are active predators, using both visual and olfactory cues for defensive behaviours, foraging, and inter-individual communication. Cuttlefish mostly rely on visual information to camouflage in their surroundings to hide from prey and avoid predators (Hanlon and Messenger, 1988), but chemical perception is also a crucial sense for the detection of both prey and predators (Hanlon and Messenger, 1996; Boal and Marsh, 1998; Boal and Golden, 1999). They can communicate with conspecifics visually (Hanlon and Messenger, 1996), and select the most sexually available partner based on chemical cues (Boal, 1996; Boal, 1997). Cuttlefish possess a centralized nervous system, and exhibit advanced cognitive abilities which have arisen independently of the vertebrates. By remembering what they have eaten, and where and how long ago they ate, cuttlefish are able to adapt their foraging behaviour according to the time of replenishment of different types of prey (Jozet-Alves et al., 2013). This study provided the first evidence of episodic-like memory in an invertebrate.

The capacity to retrieve an episodic memory is based at first on the quality of the encoding, depending on perception and sensitivity. Perception is an essential capacity for an organism to adapt its environment. It sorts appropriate information coming from the senses, to build adapted representations of the environment. This capacity to retrieve what was perceived depends on personal assessment of past internal sensations. Where episodic-like memory is based on external information (i.e., what-where-when), investigating the source *via* the retrieval of perceptive signal is based on internal information (e.g., did I smell or did I see) supported by the senses, which provides more information about a possible subjective experience of the animal ("what did I just felt?"). In this study, we assessed cuttlefish ability to discriminate between two different modalities (*i.e.,* visual and olfactory; "did I see or did I smell?") and then, to retrieve which modality was previously encountered. In experiment 1, cuttlefish were trained to discriminate visual and olfactory *stimuli* of a crab, and in experiment 2, cuttlefish were trained to discriminate visual and olfactory *stimuli* of crabs, fish, and shrimp randomly presented. Each experiment was divided into: 1) sessions of training where the cuttlefish were trained to associate a panel with a sensory modality (e.g., panel n°1 associated to olfactory

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presentation of the item), 2) transfer tests (i.e., novel item) without delay to test whether cuttlefish have learnt the rule see *vs* smell (experiment 2 only), and 3) delay tests, with a delay between presentation of the item and choice between the panels, to assess cuttlefish ability to retrieve whether they smelt or saw an item when unexpectedly asked.

1. Results

a. Experiment 1

Cuttlefish were first trained to associate panels with different graphic patterns with the modality of presentation of a crab (Figure 22a). Cuttlefish were randomly tested in three different experimental conditions: *visual condition* (crab presented inside a glass tube), *olfactory condition* (crab odour poured in the tank), and *control condition* (no visual or olfactory *stimuli* added at the beginning of the trial). Training ended when cuttlefish chose the correct panel according to the experimental condition at least 8 times out of 10 consecutive trials (Binomial test with 1/3 probability of success: p = 0.003, confidence interval: 0.44-0.97). Cuttlefish required an average of 56 trials to reach the acquisition criterion. Following training, a delay test was undertaken: a crab was presented using either olfactory or visual cues. After a delay, only panels associated to visual and olfactory conditions were placed in the tank to test cuttlefish ability to retrieve whether they smelt or they saw the crab before (Figure 22b; for details see Methods). Results showed that all cuttlefish chose the correct panel according to the modality of presentation of the crab encountered 1h before (Binomial test: p = 0.0039, confidence interval: 0.66-1). Cuttlefish were tested the following day with a 3h delay, and most of them correctly retrieved the modality of presentation of the crab encountered before (p = 0.039, confidence interval: 0.52-0.99). However, during a delay transfer test (novel item; Figure 22c), cuttlefish were not able to retrieve the panel corresponding to the presentation of a novel prey after 1-hour and 3-hours delays (Binomial test: 1-hour delay, p = 1, confidence interval: 0.21-0.86; 3-hours delay, p = 0.50, confidence interval: 0.075-0.70).

Billard, P., Clayton, N. S., & Jozet-Alves, C. (2020). Cuttlefish retrieve whether they smelt or saw a previously encountered item. Scientific Reports 10:5413. DOI: 10.1038/s41598-020-62335-x

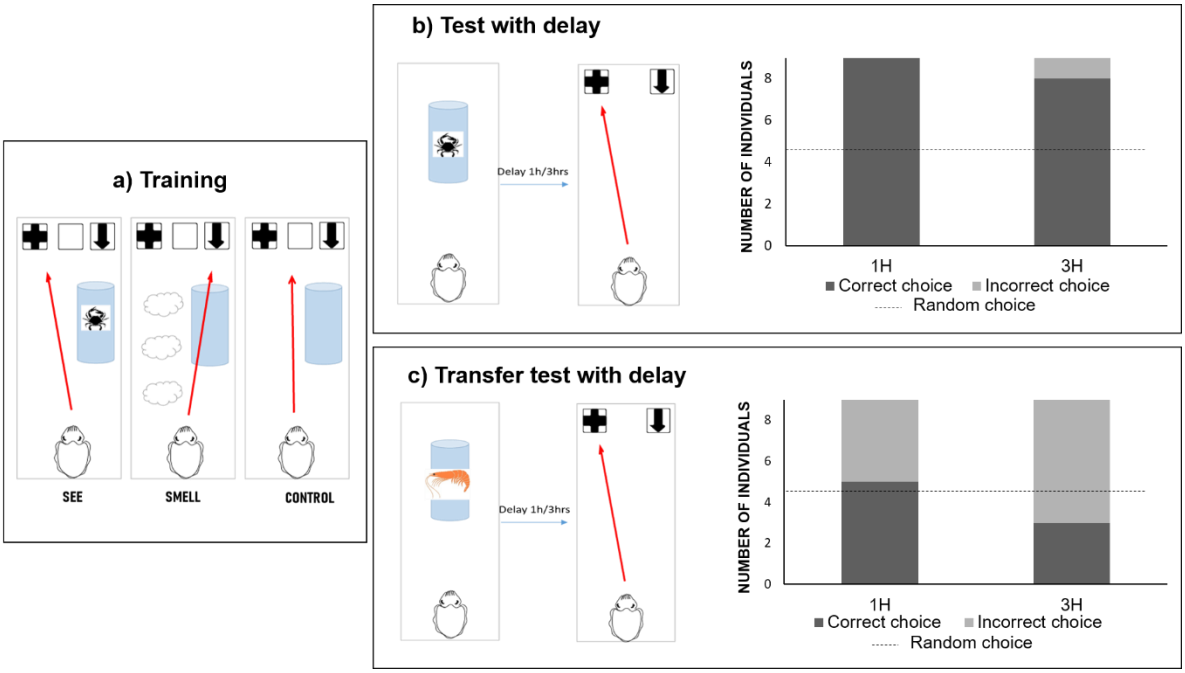

Figure 22 Experimental procedures and results for Experiment 1. a) Training session: cuttlefish were presented with three different experimental conditions. SEE condition where the visual stimulation of a crab was associated with the left panel (i.e., panel n°2); SMELL condition where the olfactory stimulation of a crab was associated with the right panel (i.e., panel n°1); CONTROL condition with no presentation of visual and olfactory stimulation, associated with the central panel (i.e., panel n°3). b) Delay test: cuttlefish were presented with visual or olfactory stimulation of a crab. After a delay, they had the opportunity to make a choice between panel n°1 and panel n°2. All the cuttlefish chose the correct panel after 1h delay, and the majority of cuttlefish chose the correct panel after 3hrs delay. c) Delay transfer test: cuttlefish were presented with visual or olfactory stimulation of a shrimp. After a delay they had the opportunity to make a choice between panel n°1 and panel n°2. 5 cuttlefish passed the transfer test after 1h delay, and 3 cuttlefish passed the transfer test after 3hrs delay.

b. Experiment 2

In experiment 2, cuttlefish were trained with three different items (*i.e.*, fish, crab, and shrimp, Figure 23a). All cuttlefish reached the learning criterion (Binomial test with 1/3 probability of success: p = .003, confidence interval: 0.44-0.97). Once cuttlefish reached the learning criterion, transfer tests were realized (without delay between presentation of the item and choice of a panel; Figure 23b). Once cuttlefish succeeded these transfer tests, they were tested with a 3h delay (i.e., delay transfer test; for details see Methods; Figure 23c). All the cuttlefish (five out of five) tested were able to retrieve the correct panel linked with the presentation of the new items after 3-hours delay.

Billard, P., Clayton, N. S., & Jozet-Alves, C. (2020). Cuttlefish retrieve whether they smelt or saw a previously encountered item. Scientific Reports 10:5413. DOI: 10.1038/s41598-020-62335-x

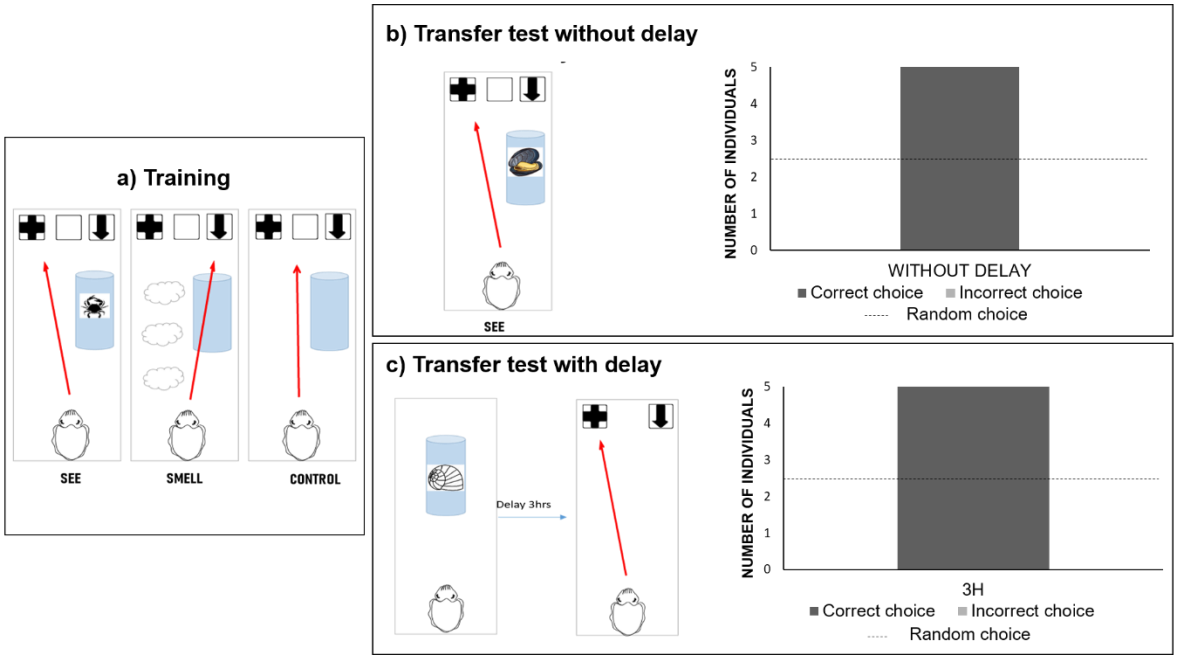

Figure 23 Experimental procedures and results for Experiment 2. a) Training session: the experimental set-up was identical to the first experiment, except that cuttlefish were randomly presented with visual and olfactory stimulations of fish, crabs, and shrimp. b) Transfer tests without delay: cuttlefish were presented with visual and olfactory stimulation a novel item never encountered before. All the cuttlefish managed to pass this transfer test without delay. c) Delay transfer test: cuttlefish were presented with a novel item. After 3hrs delay, cuttlefish had the opportunity to make a choice between panel n°1 and panel n°2. All the cuttlefish passed the transfer test with delay.

2. Discussion

We showed that cuttlefish are able to learn a discrimination rule based on two sensorial modalities (vision *versus* olfaction) and are able to retrieve the modality of presentation of an item presented before a long-term delay.

In Experiment 1, cuttlefish were able to retrieve the modality of presentation of a crab encountered 1-hour and 3-hours before. However, they were not able to perform the task with a novel prey (i.e., shrimp). This result suggests that cuttlefish likely used an associative-learning based strategy to perform the task, associating the crab's characteristics (i.e., odour of crab, sight of crab) with the visual cues, instead of generalizing the discrimination rule "see *vs* smell". To facilitate learning of this general rule, we ran Experiment 2 using several items during training (i.e., crabs, shrimps, and fish). We ran a transfer test without delay after training to establish whether the cuttlefish were able to generalize the rule to new items. In this second experiment, the cuttlefish were able to generalize their discrimination learning to new items, showing that they extracted the rule "see *versus* smell". This last result shows that cuttlefish did not use lower-level cognitive processes to solve the task as they did in the first experiment.

Billard, P., Clayton, N. S., & Jozet-Alves, C. (2020). Cuttlefish retrieve whether they smelt or saw a previously encountered item. Scientific Reports 10:5413. DOI: 10.1038/s41598-020-62335-x

To our knowledge, our study is the first to demonstrate the ability to discriminate between two sensory modalities in animals. Under the visual modality, several studies showed animals' capacity to discriminate between colours (e.g., bees, Giurfa, 2004; chimpanzees, Jarvik, 1956; weanling pigs, Tanida et al., 1991; seals, Wartzok and McCormick, 1978; horses, Smith and Goldman, 1999; cats, Meyer and Anderson, 2008; ravens, Range et al., 2008), shapes or positions (e.g., mice, Brigman et al., 2005; octopus, Sutherland, 1958), and movements (e.g., pigeons, Dittrich et al., 1998). The ability to discriminate between olfactory cues was also shown in several species using odours and flavours (e.g., rats, MacKintosh et al., 1991; Cohen et al., 2009; bees, Galizia and Menzel, 2000; dogs, Hepper, 1988; bats, De Fanis and Jones, 1995; pandas, Swaisgood et al., 2000; pigs, Mendl et al., 2002). Other studies used multimodal cues to evaluate their interaction or facilitation effect on a discrimination task. For instance, Verbaal and Luksch (2016), investigated the effect of audiovisual *stimuli* in comparison to audiory and visual *stimuli* alone on discrimination capacities in chicken. Studies have yet to investigate the animal's capacity to discriminate the sensation *per se* (i.e., do you *see* or do you *smell*?). Previous studies focused on one sensorial modality at a time (e.g., visual *or* olfactory), or used multimodal cues for other purposes. Our study also brings new insights on cephalopods' discrimination abilities. It has been shown that cuttlefish can visually discriminate brightness, substrate texture (Hanlon and Messenger, 1988), graphic patterns (Hvorecny et al., 2007; Jozet-Alves et al., 2008), and olfactory discriminate odours from congeners, food or predators (Boal and Golden, 1999; Mezrai et al., 2018). But it is the first time that a study shows cuttlefish ability to recognize and discriminate between olfactory and visual *stimuli*.

In item *versus* source tasks used to investigate source-memory in humans, participants are not aware that they will be asked about the source of information at the time of encoding. In our study, cuttlefish were trained to repeatedly choose the correct panel according to the modality of presentation of an item (*i.e.,* visual or olfactory modalities). This experimental design induced learning of a semantic rule: *i.e.,* association sensory modalities/panels. At test, using a new item and adding a delay allowed us to unexpectedly ask cuttlefish whether they smelt or saw the item before. This procedure was designed to avoid cuttlefish to explicitly encode the sensory modality at the time of presentation of the item, as cuttlefish was not aware that it will be asked to answer the question see *vs* smell later. Nevertheless, it is possible that cuttlefish chose by familiarity the correct panel according to the last modality (*i.e.,* olfactory or visual) sensed when the item was presented. In further studies, the effect of familiarity will be countered by successively exposing cuttlefish to two items (one visually and the other olfactory)

Billard, P., Clayton, N. S., & Jozet-Alves, C. (2020). Cuttlefish retrieve whether they smelt or saw a previously encountered item. Scientific Reports 10:5413. DOI: 10.1038/s41598-020-62335-x

in different contexts. At test, cuttlefish will be asked to retrieve the modality of presentation of the first or second item according to the context, to control sensory memory trace (Cheng et al., 2016).

Our study provides the first evidence that cuttlefish are able to discriminate and retrieve their own visual and olfactory sensations. This finding is a real advance in the study of episodic cognition in animals. The classical debate as to whether mental time travel is unique to humans opposes 1) the capacity of subjective experience observed in humans, 2) to the capacity of "simply" form sequential mnemonic representations of personal past episodes (Clayton and Dickinson, 1998). In classical episodic-like memory tasks, subjective experience is not assessed as animals need to retrieve external information only (e.g., what-where-when, Clayton and Dickinson, 1998). In absence of language, it is still impossible to investigate subjective experience in animals. However, our design might be useful to approach the question of subjectivity as it is based on animals' capacity to retrieve an internal information from a previous event (*i.e.,* own perception). The source-monitoring framework specifies that an episodic memory is retrieved when *several* signals are brought back in mind. In our experiment, cuttlefish were trained to retrieve a single perceptive signal. In future studies, it would be necessary to test whether cuttlefish are able to remember different signals in an integrate representation, such as for instance a perceptive and a contextual signal.

Billard, P., Clayton, N. S., & Jozet-Alves, C. (2020). Cuttlefish retrieve whether they smelt or saw a previously encountered item. Scientific Reports 10:5413. DOI: 10.1038/s41598-020-62335-x

3. Methods

a. Ethical statement

Experiments were carried out in accordance with directive 2010/63/EU (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 (Comité d'Ethique Normandie en Matière d'Expérimentation Animale, CENOMEXA; agreement number 54).

b. Subjects

The experiments were carried out in sub-adult European common cuttlefish (*Sepia officinalis*) ranging in age from 3 to 6 months at the start of experiment 1 (N = 9) and from 9 to 12 months at the start of experiment 2 (N = 6). Five out of the six cuttlefish tested in experiment 2 were reused from experiment 1. Cuttlefish were reared from eggs collected in the English Channel, at the CREC (Centre de Recherches en Environnement Côtier – Marine Station of the University of Caen, Luc-sur-Mer, France). Cuttlefish were housed individually in grey plastic tanks (80x60x40cm) with natural circulating seawater (temperature: 15 ± 1°C). Cuttlefish were maintained under artificial light conditions (12L:12D cycle) and were fed daily with live crabs (*Carcinus manenas*) and shrimp (*Crangon crangon*) of suitable size before starting the experiments. One cuttlefish was removed from the experiment before the final test because it started to display an unusual swimming behaviour.

c. Experimental conditions

The panels used in the experiments consisted of 10 cm white plastic squares with or without a black geometric shape in the middle: panel n°1 pictured a graphic arrow, panel n°2 pictured a cross, and panel n°3 was devoid of drawing. Cuttlefish were trained to associate each panel with different experimental conditions:

- SMELL condition: Association panel n°1 / olfactory stimulation. Cuttlefish were trained to go close to the panel n°1 when seawater with a *stimulus* odour was poured in the tank (*i.e.,* experiment 1: odour of crab; experiment 2: odour of crab, fish or shrimp). To prepare olfactory stimulus for SMELL conditions, items were placed in a bucket with seawater so that their smell spread in the water (about one liter of water for one adult crab (*Carcinus maenas*), three liters for one adult fish (*Dicentrarchus labrax*), and one liter for five adult shrimp (*Crangon crangon*)).

Billard, P., Clayton, N. S., & Jozet-Alves, C. (2020). Cuttlefish retrieve whether they smelt or saw a previously encountered item. Scientific Reports 10:5413. DOI: 10.1038/s41598-020-62335-x

- SEE condition: Association panel n°2 / visual *stimulus*. Cuttlefish were trained to go close to the panel n°2 when a visual *stimulus* was presented inside the glass tube (*i.e.,* experiment 1: one live crab; experiment 2: one live crab, juvenile fish or shrimp).
- CONTROL condition: Association panel n°3 / absence of additional olfactory or visual stimulation. Cuttlefish were trained to go close to the panel n°3 when no additional visual *stimulus* (*i.e.,* glass tube empty) or olfactory *stimulus* (*i.e.,* natural seawater without *stimulus* odour poured in the tank) was presented. Control condition is necessary to make cuttlefish learn the association between panel n°1 / olfactory stimulation, and not panel n°1 / nothing in the glass tube.

d. Procedure

i. Experiments 1&2: Pre-training: learning to approach a panel to get food

Step 1: Familiarization. To familiarize cuttlefish with the presence of panels inside their tank, the panel n°3 was placed in their home tank during each feeding session during a week.

Step 2: Approaching a panel to get a food reward. The panel n°3 was placed in the tank; after 60 seconds, a prey was placed just in front of it. If the cuttlefish did not catch the prey within 3 min, both the panel and the prey were removed from the tank. This procedure was repeated four times a day. When a cuttlefish went repeatedly close (*i.e.,* less than 10 cm) to the panel before placing the prey in the tank, cuttlefish started training. We considered that cuttlefish had learned the task when they went close to the panel in less than 60 seconds after it was placed inside their home tank, at least 8 times in 10 consecutive trials.

ii. Experiments 1&2: Training: learning to approach a distinct panel according to the experimental condition

Cuttlefish were tested four times a day. Each experimental condition was presented in randomized order (StatTrek.com). At the beginning of a trial, whatever the experimental condition, the same gestures were repeated by the experimenter: 1) a glass tube (higher than the water surface) with or without visual *stimulus* inside was gently placed inside the tank, 2) a 500 mL beaker full of natural seawater with or without additional olfactory *stimulus* was carefully poured in the tank, and 3) the three panels were placed along one of the walls of the tank. Cuttlefish were rewarded (one shrimp or one crab) when they came, closer than 10 cm, in front of the correct visual cue. When the prey was caught by the cuttlefish, the glass tube and the panels were removed from the tank. When the first panel approached by cuttlefish was the correct one according to the experimental condition, this was considered as a correct choice.

Billard, P., Clayton, N. S., & Jozet-Alves, C. (2020). Cuttlefish retrieve whether they smelt or saw a previously encountered item. Scientific Reports 10:5413. DOI: 10.1038/s41598-020-62335-x

When cuttlefish failed to go close to the correct panel within 4 minutes, the three panels and the glass tube were removed from the tank. When cuttlefish approached the correct cue but not at first or did not approached it within 4 minutes, this was considered as incorrect choice. Cuttlefish were trained until they reached a learning criterion established as eight correct choices out of ten consecutive trials (Binomial test: probability to choose the correct visual cue: probability of success = 1/3; $p = 0.003$).

iii. Experiment 1: Test phase

To make sure cuttlefish choose a panel according to the kind of stimulation encountered before the delay and not currently experiencing, only panels n°1 (SMELL) and n°2 (SEE) were introduced in the tank at tests and transfer tests with delay.

Delay test: Have you seen or smelt a crab before? When the learning criterion was reached, the test phase began. For the first test trials, a delay was introduced between the presentation of the *stimulus* (*i.e.,* crab odour poured in the tank or crab placed inside the glass tube) and the introduction of the panels inside the tank. Panels n°1 (SMELL) and n°2 (SEE) were introduced in the tank. Each cuttlefish was tested once with two different delays (1 hour and 3 hours), one test was performed per day (day 1: 1hour; day 2: 3hours delay), with some trials were ran in-between. The experimental conditions (SMELL or SEE) used were randomly chosen.

Delay transfer tests: Have you seen or smelt a shrimp before? The procedure described before was repeated using a shrimp as a *stimulus* instead of a crab. Each cuttlefish was tested once with two different delays (1 hour and 3 hours), the experimental conditions (SMELL or SEE) used being randomly chosen.

iv. Experiment 2: Test phase

Transfer tests without delay: Do you see or smell? When the learning criterion was reached, cuttlefish were first presented with a transfer test once to check whether they actually learnt to distinguish SMELL *versus* SEE conditions. In this test, the procedure used was the same than during training repeated *once* with a novel *stimulus* (*e.g.,* mussel, snail, seaweed, etc.). If the transfer test was successful (*i.e.,* the cuttlefish choose the panel associated with the modality of presentation of the prey) cuttlefish went to the next step (*i.e.,* delay transfer test). If the transfer without delay was not successful, cuttlefish went back to training until they reached the learning criterion another time, and another transfer test without delay was realized (with a novel prey each time).

Billard, P., Clayton, N. S., & Jozet-Alves, C. (2020). Cuttlefish retrieve whether they smelt or saw a previously encountered item. Scientific Reports 10:5413. DOI: 10.1038/s41598-020-62335-x

Delay transfer tests: Have you seen or smelt an item before? Once cuttlefish successfully passed the transfer test without delay, they were tested with a delay. The procedure used was the same as described in "Delay transfer test" for experiment 1, except: that the *stimulus* presented was neither used for training nor transfer tests without delay, and that only one delay interval was used: three hours.

e. Statistical analyses

All data were analysed with non-parametric tests and computed using R software (version 3.5.1). We determined a learning criterion of 8 correct answers out of 10 consecutive trials with a probability of success of 1/3. To analyse whether most cuttlefish significantly chose the correct panel after the delay, we used exact binomial tests (binom.test function on R). *P* values and confidence intervals were reported.

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II. Exploration of source-memory in Eurasian jays

A new paradigm for assessing discriminative learning and incidental encoding of task-irrelevant contextual cues in Eurasian jays

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Abstract

In absence of agreed non-linguistic measures of the phenomenological consciousness that accompany the experience of episodic memory in humans it is impossible to establish whether episodic-like memory, the ability to recall what, where and when of a past event, really is like episodic memory. One way forward is to investigate another crucial element of episodic memory that can be tested in animals: the incidental nature of episodic memories where the experience is encoded automatically without any intention to encode it. Most studies in animal cognition have pre-exposed the animals with the to-be-incidentally encoded stimuli before the actual test and the animals may have deliberately encoded it. To address this issue, our study adopts two new procedures 1) a visual discrimination task in Eurasian jays where a task-irrelevant contextual cue is presented; 2) an incidental encoding test assessing jay's capacity to incidentally encode this cue. During the visual discrimination task, jays were trained to discriminate between two types of pictures by choosing to land on coloured left or right perches to receive a reward. Jays were presented with a task-irrelevant contextual cue consisting of geometrical coloured shapes hung on the wall of the testing room. The incidental encoding test revealed that all males incidentally encoded the contextual cue, whereas females, even though they were quicker to learn the initial discrimination task, seemed to behave at random during this final test. Even though the number of tested individuals is low, these unexpected results might suggest the existence of sex dimorphism in cognition in this species.

Keywords: Discriminative learning – Episodic memory – Incidental encoding – Sex differences – Eurasian jays

Introduction

Episodic memory was originally defined by Tulving in terms of temporal-spatial relations between events (i.e., what happened, when, and where, or rather the spatiotemporal relations between events; Tulving 1972). Later, Tulving included aspects of phenomenological consciousness, namely autonoetic awareness (i.e., the awareness that we live in our own present, that our memories belong to our own past and are different from others, and that we can imagine our own future, Tulving 1983), and chronesthesia (i.e., the conscious awareness of subjective time, Tulving 2009). In humans, episodic memory is typically investigated through verbal reports of personal past events. As animals cannot speak, Clayton and collaborators developed three behavioural criteria (i.e., content, structure, and flexibility) to investigate what they called the episodic-like memory because these criteria focus on the non-phenomenological aspects of episodic remembering (Clayton and Dickinson 1998, Clayton et al., 2001a, 2003a). Based on Tulving's original definition of episodic memory (i.e., that episodic memories can be temporally and spatially dated, Tulving, 1972), Clayton and Dickinson (1998) defined the content of episodic-like memories in terms of what happened, where, and when based on a trial-unique experience, and argued that the content of such memories needs to form an integrated structure in which what, where and when information is bound together and can be flexibly deployed (Clayton et al., 2001b).

In their seminal study, Clayton and Dickinson (1998) showed that jays remembered what type of food they cached (i.e., wax worms, peanuts), where (i.e., the location in the tray) and how long ago (i.e., after a 4-hour or 124-hour delay). In another study, authors showed that inspections of caches depended on the incentive value of the food at recovery and not at caching ruling out an explanation in terms of familiarity (Clayton and Dickinson, 1999b). Later, Clayton and collaborators established that the what-where-when criterion formed an integrated representation in the jays' memory (Clayton et al., 2001b), confirming the second criteria of episodic-like memory in jays (i.e., structure, the capacity to form an integrated representation of what-where-when). They also revealed that this integrated representation could be used flexibly (Clayton et al., 2003b), validating the third behavioural criteria of episodic-like memory in jays (i.e., flexibility). Furthermore, the jays' performance in these experiments could not be explained by direct forgetting (de Kort et al., 2005). Finally, the jays were able to use past experiences to spontaneously plan for future events (Raby et al., 2007) and in ways that clearly demonstrated that the birds were acting for future motivational needs not current ones (Correia et al., 2007; Cheke and Clayton, 2012).

Billard, P., Jozet-Alves, C., Clayton, N. S. (in revision in Animal Behavior and Cognition) A new paradigm for assessing discriminative learning and incidental encoding of task-irrelevant contextual cue in Eurasian jays.

The what-where-when paradigm was adapted in various species such as apes (Martin-Ordas et al., 2010), rodents (Babb and Crystal, 2006), other corvids (e.g., magpies, Zinkivskay et al., 2009), and cephalopod molluscs (Jozet-Alves et al., 2013). In these studies, animals are trained to learn certain specificities about the role of time and the relevance of "when" (e.g., peanuts do not perish, whereas worms are fresh after a short delay but decay after a long delay). Animals learn that they will be given the opportunity to search for these hidden food rewards after a variable delay (thus the importance of also remembering what and where). The critical tests involve a trial-unique feature that requires the animal to attend to what was hidden where and when on any given day. Given these training criteria, might the animals learn to know what information they need to focus on and *intentionally* encode it to obtain a later reward? If the animals do intentionally encode the elements, predicting that they may well be asked later, then the recall of this type information might not be episodic but instead be based on semantic knowledge of what happened where and when, in much the same way that we know when we were born without having an experiential memory of our birth.

Zentall (2001, 2008) argued that repeated training results in the acquisition of a set of rules may create expectations and it is possible that the animals deliberately attend the stimuli to save the information for later. When the information is encoded incidentally, without any expectation that they will be asked to retrieve the information, the only way to retrieve this information is to retrieve an episodic memory of the previously encountered information. That said, episodic memories can be formed also on the basis of focussed attention and deliberate encoding, yet it is impossible to establish whether the animals are creating episodic memories or semantic memories after such encoding. In humans, the distinction between semantic and episodic recall can be revealed by asking participants whether they remember an item's occurrence in a list, or whether they only know that the item was previously encountered without being able to give any contextual detail (Tulving, 1985). One way to reduce the likely occurrence of semantic storage and recall of information in animals would be to use an incidental encoding paradigm to avoid any deliberate encoding, where the animals are unexpectedly asked to retrieve a contextual detail on which they did not focus previously. For instance, rats remembered the context in which items occurred (Panoz-Brown et al., 2016).

In humans, episodic memories are usually encoded incidentally without a specific intention to do so. For instance, I am able to remember that I went running last week-end with my friends, and that one of these friends was wearing a black jumper, that the weather was cold, and that we were running in muddy pathways, although I did not deliberately choose to learn these

Billard, P., Jozet-Alves, C., Clayton, N. S. (in revision in Animal Behavior and Cognition) A new paradigm for assessing discriminative learning and incidental encoding of task-irrelevant contextual cue in Eurasian jays.

details. The encoding and recall of episodic memories are unique in the sense that the rememberer is able to retrieve the entire event (often involving lots of details) whether or not the elements composing the event were deliberately encoded or the focus of attention (Morris and Frey, 1997; evidence for remembering a stream of events in rats (Panoz-Brown et al., 2018; in apes: Kano and Hirata, 2015). Incidental encoding then occurs when information apparently unimportant at the time of encoding is encoded and retrieved in a subsequent unexpected test (Crystal, 2018). Zentall (2001, 2008), used the unexpected question to confront the animals with their ability to retrieve previous information, encoded without knowledge that it might be useful later. The unexpected nature of the question implies that the retrieval of previous information does not rely on food-reinforcement as the animal was not encouraged to learn this information.

In animals, only a few studies have investigated the ability to encode incidental information. Zentall first raised the issue in pigeons (Zentall et al., 2008). Subsequently, several studies were run on dogs (Fujita et al., 2012; Fugazza et al., 2016; Sluka et al., 2018), cats (Takagi et al., 2017), squirrel monkeys (Goldberger et al., 1980), and rats (Zhou et al., 2012; Allen et al., 2020). In these studies, the to-be-remembered item is the centre of attention at the time of encoding, but the animal is supposedly not aware that their memory will be tested. In the study of Fujita et al., (2012) later adapted by Takagi et al., (2017) and Sluka et al., (2018), dogs and cats were presented with trays disposed in a fan shape and were allowed to eat from two of them. At test, the animals had the opportunity to explore similar trays, and the first tray revisited by animals was recorded (Fujita et al., 2012; Takagi et al., 2017). Authors argued that this procedure measures animals' ability to incidentally encode the spatial characteristics of the trays. However, as the emplacement of the trays is directly linked to the tray itself, animals might have intentionally associated tray features and food for later visit. In another study, dogs were extensively trained to respond to the command "do as I do" (i.e., dogs reproduce an action performed by their owner; Fugazza et al., 2016). Once this training was completed, dogs were trained to sit down after witnessing an action of their owner. At test, dogs were unexpectedly asked to imitate the action of the owner (i.e., owner says "do as I do"). Authors argued that dogs had incidentally encoded the characteristics of the gesture seen as dogs were rather being expected to sit down thereafter and not being asked to imitate their owner's action. As dogs were firstly extensively trained to answer the command "do as I do", an alternative explanation would be that dogs would keep on focussing their attention on the owner's action during the second training, and thus, intentionally encoded the information of the action (for a review on

Billard, P., Jozet-Alves, C., Clayton, N. S. (in revision in Animal Behavior and Cognition) A new paradigm for assessing discriminative learning and incidental encoding of task-irrelevant contextual cue in Eurasian jays.

this paper see Crystal 2016; see also the recent study of Fugazza et al., 2020 on dog's capacity to categorize in absence of specific training). In the Zhou et al. (2012) and Zentall et al. (2008) studies, to perform the incidental encoding test, animals were required to unexpectedly retrieve elements they were used to focus on during previous experiments (e.g., whether food was encountered or not). All these studies used the to-be-incidentally-encoded material as part of a training or pre-exposure phase and the material is directly linked to the task. This pre-exposure to the incidental material may have led the animals to pay more attention to it than it would have been the case if the material was not directly part of the task, and possibly have intentionally encoded it. To avoid this, it would be relevant not to involve this to-be-incidentally-encoded information as part of the task but as a non-relevant context. This procedure will prevent animals to intentionally focus their attention on it, just like we do when we witness an event without knowing that we will be asked about one of its features later.

Corvids possess the largest brain relatively to their size of any other birds (Clayton and Emery, 2005). They present a social organization where the young are taught the essential skills to survive. They also exhibit impressive capacities to solve problems finding innovative solutions, such as the manufacturing of tools (Bird and Emery, 2009) and complex foraging behaviours (e.g., development of strategies to counter potential pilferers, Clayton et al., 2007). More specifically, the Eurasian jay has been showed to be able to use tools (Cheke et al., 2011), to flexibly choose what food to share according to what the partner has eaten before (Ostojic et al., 2013), and to overcome their current desire to anticipate the food they will recover the close future (Cheke and Clayton, 2012). In the what-where-when paradigm, jays were trained to learn the specifics of the task (i.e., time decay of different food items), and they might have focussed their attention on the spatial-temporal features of the event to succeed such tasks. Even if episodic memory can be considered as a comprehensive recording of events with features encoded both intentionally (*via* focussed attention) and incidentally, testing incidental learning abilities in jays will be useful to go further in the understanding of the cognitive mechanisms involved in episodic cognition in birds. In this aim, it will appear important to test whether jays are also able to retrieve some features of previously experienced events they were not explicitly attending to at the time of the event. As episodic cognition allows one to anticipate the future and to retrieve the past based on incidental encoding, we postulate that jays would be able to incidentally encode a contextual cue. Whereas scrub-jays have been largely studied in episodic-like memory tasks, Eurasian jays have not been yet tested. In an evolutionary and comparative

perspective, investigating Eurasian jay's ability for episodic cognition is of particular relevance to bring further knowledge of episodic cognition abilities in corvids.

In this study, we designed a novel method to test the Eurasian jays' ability to incidentally encode a contextual cue by avoiding a focus on the to-be-incidentally encoded material before the actual test. More specifically, we asked whether they incidentally encode non-relevant contextual cues while performing a simple discrimination task. Our experimental design is composed of three steps:

1) Training/ Discrimination task

Firstly, the jays were trained to discriminate between two types of pictures differing in several features (either coloured pictures of birds oriented in portrait, or black-and-white pictures of trees oriented in landscape) and associate each type of pictures with perches of different colours (either blue or yellow, respectively located on the left and on the right part of the picture) to get a reward. As the study of discriminative learning was not the main focus of our experiment, several characteristics were confounded to facilitate the learning of the discrimination task. While performing this simple discriminative task, they were simultaneously exposed to non-relevant contextual cues (geometrical coloured shapes, see Figure 24).

2) Transfer session

Once the acquisition criterion had been reached, jays were successively tested with two pictures (one of each type) never encountered during training. If the jays gave the correct answer for both pictures, they went to the incidental encoding test. If they fail to choose the correct perch for both pictures, they went back to training.

3) Incidental encoding test

The incidental encoding test was composed of three phases: two presentation phases and one test phase. During the two presentation phases, the perches were not provided in the testing compartment. During the first presentation phase, jays were presented during 5 minutes with a picture (e.g., new picture of tree), and a contextual cue (e.g., blue circle) non-encountered before. Afterwards, the picture and the contextual cue were removed. During the second presentation phase, jays were presented during 5 minutes with the other type of picture (e.g., new picture of bird) and another contextual cue (e.g., purple triangle) non-encountered before. The test phase started 5 minutes after the end of the second presentation phase. One of the two

Billard, P., Jozet-Alves, C., Clayton, N. S. (in revision in Animal Behavior and Cognition) A new paradigm for assessing discriminative learning and incidental encoding of task-irrelevant contextual cue in Eurasian jays.

contextual cues (i.e., blue circle or purple triangle) was placed back in the testing room as well as the two perches. The jays then had the opportunity to land on one of the perches (Figure 4).

During this incidental encoding test, the jays are unexpectedly asked which type of picture was encountered in presence of a particular contextual cue. We predicted that if the jays were able to incidentally encode the contextual cues during the presentation phases, they should be able to retrieve which type of picture was presented alongside the contextual cue, and land on the corresponding perch. As the jays were not trained to pay attention to these contextual cues while performing the discrimination task, we hypothesized that the birds should not expect to be asked to retrieve these contextual cues in the future and would not have intentionally associated them with the type of picture they were exposed to. The question "which picture did you see in this context" being unexpected, their capacity to retrieve which picture was encountered with which contextual cue might be explained by incidental encoding.

Billard, P., Jozet-Alves, C., Clayton, N. S. (in revision in Animal Behavior and Cognition) A new paradigm for assessing discriminative learning and incidental encoding of task-irrelevant contextual cue in Eurasian jays.

1. Method

a. Subjects:

11 adult Eurasian jays (*Garrulus glandarius*, males: n = 6, females: n = 5) participated in this study. The jays ranged from 5 to 14 years of age, and were captured from the wild when they were chicks. The experiment was approved by the University of Cambridge (University of Cambridge Ethical review number: ZOO68/19). The birds were housed in three different aviaries (aviary 1: n = 3; colony 2: n = 2; aviary 3: n = 6) each of which comprised of outdoor aviaries measuring 20 x 6 x 3 m, length, width, height in addition to 2 x 1 x 2 m indoor testing compartments. Birds were fed a maintenance diet of soaked biscuits, cheese, seeds, nuts, and fruits and had ad libitum access to water.

b. Materials:

Two types of pictures (dimensions: 210 mm x 297 mm) were used in our experiments (Figure 24):

- Coloured pictures of birds (e.g., kingfisher, robin, pigeon) oriented in portrait
- Black-and-white pictures of trees (e.g., trees with and without leafs) oriented in landscape

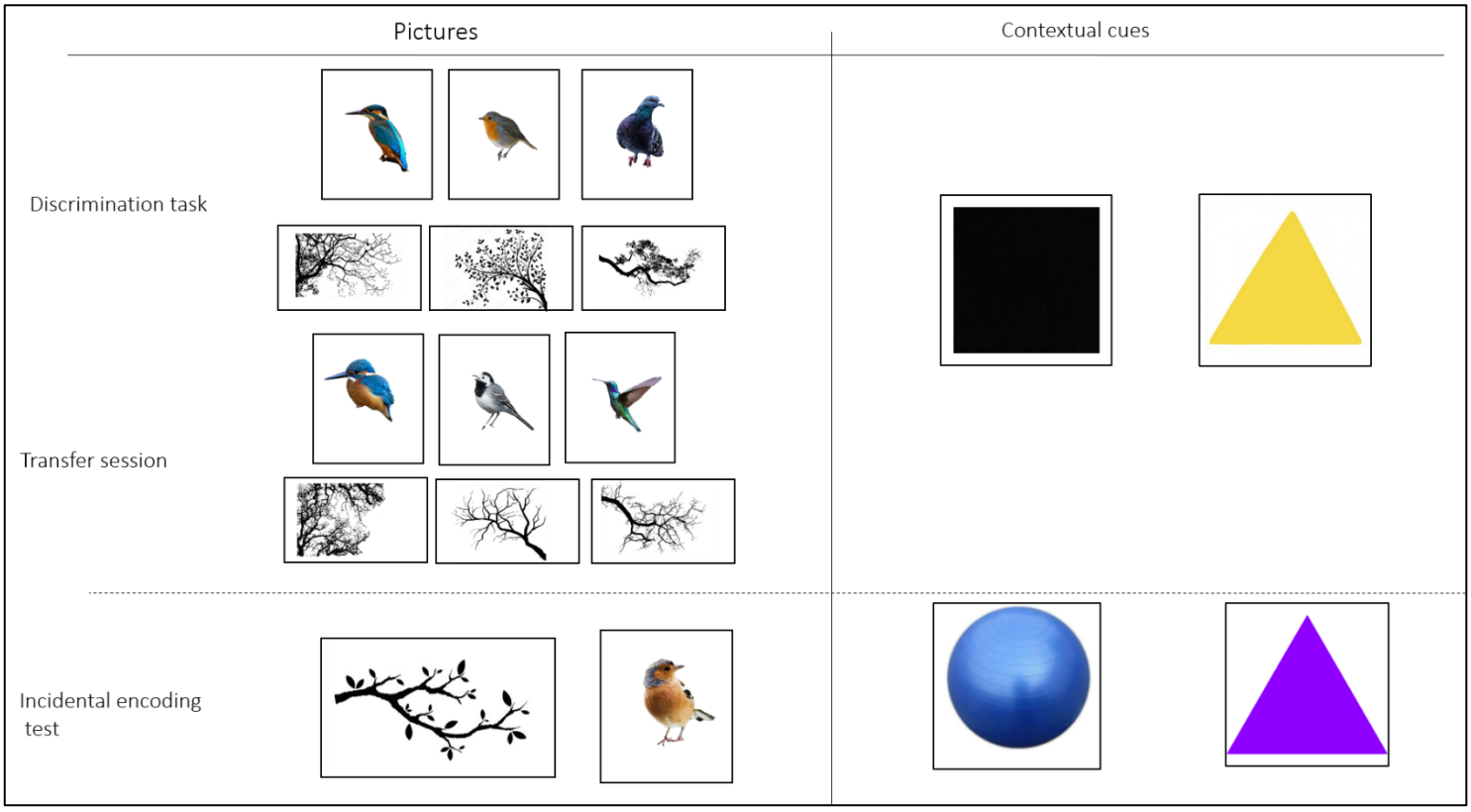

Figure 24 Pictures and contextual cues used during the discrimination task, the transfer session, and the incidental encoding task.

Different pictures were used for the three steps of our experiment: training/discriminative task (three pictures of each type), the transfer sessions (one picture of each type for each session), and the incidental encoding test (one picture of each type). The two types of pictures were associated with either a blue or a yellow perch, one in the left and one in the right hand side (e.g., blue perch on the left associated with pictures of birds and yellow perch on the right associated with pictures of trees, and vice versa). The associations between the type of picture, the colour of the perch and the right/left positions of the coloured perches were counterbalanced to ensure that the overall response of the birds was not controlled by side biases or colour preferences.

c. Contextual cue used for the incidental encoding:

The contextual cues used for our experiments (Figure 24) were sheets of paper (dimensions: 210 mm x 297 mm) representing geometrical shapes (e.g., squares, triangles, circles, etc.) of different colours (e.g., black, purple, light blue, etc.) and were fixed on the walls or the door of the testing compartment. Contextual cues used during training and transfer session differed from contextual cues used during the incidental encoding test.

d. Procedure:

Testing took place in the compartments attached to the aviary (Figure 25). The experiment was organized in three steps.

Billard, P., Jozet-Alves, C., Clayton, N. S. (in revision in Animal Behavior and Cognition) A new paradigm for assessing discriminative learning and incidental encoding of task-irrelevant contextual cue in Eurasian jays.

Figure 25 Examples of the experimental set-up used during transfer session in the testing room of a male jay called Caracas.

Training / discrimination task:

Each training session (one per day) was composed of 10 trials, and was performed in the morning (Figure 26). One of two contextual cues (i.e., geometrical shape of a black square or a yellow triangle) was randomly (randomization across individuals and training sessions) placed in the testing compartment before the beginning of each training session. The contextual cue remained the same all along the training session. The contextual cues (i.e., black square or yellow triangle) were randomized across sessions of training. During a trial, the experimenter presented one picture (e.g., picture of a bird) equidistant to a blue and a yellow perch on a Plexiglas window situated on the door of the testing compartment. The perches were located on both sides of the picture. The jays, having been previously trained to hop on the perches, were rewarded (meal worm) only if they landed on the perch associated with the type of picture presented (e.g., blue perch with picture of a bird). If jays land on the perch associated with the picture presented (e.g., blue perch with picture of tree) the animals were rewarded (meal worm). If not, jays were not rewarded and the picture was removed. The next trial started when a new picture of bird or tree was presented. Training continued until the birds reached a learning criterion established as 12 correct choices out of 15 consecutive trials (number of correct answers statistically different from random choices: binomial test: $p = .035$). Once the criterion reached (at the end or within a training session), the training session immediately ended and the jays went to the transfer session.

Billard, P., Jozet-Alves, C., Clayton, N. S. (in revision in Animal Behavior and Cognition) A new paradigm for assessing discriminative learning and incidental encoding of task-irrelevant contextual cue in Eurasian jays.

Transfer session:

The transfer session, composed of two trials, was realized the day after the jays reached the learning criterion (Figure 26). This session aimed to test whether jays understood the general rule to be used to discriminate the two types of pictures: i.e., black-and-white landscape-oriented pictures of trees versus coloured pictures of birds oriented in portrait. Jays were tested with two pictures not encountered during training. The order of presentation of the pictures (e.g., trial 1: picture of a bird; and trial 2: picture of a tree) was randomized between birds. All along the transfer session, one of the contextual cues used during training was presented (the contextual cue used was randomized among birds).

If jays failed at least once to choose the correct perch over the transfer session, they went back to the previous step of our experiment (i.e., training/discrimination task) until they reach once again the learning criterion. If jays managed to pass both trials, they went to the incidental encoding test.

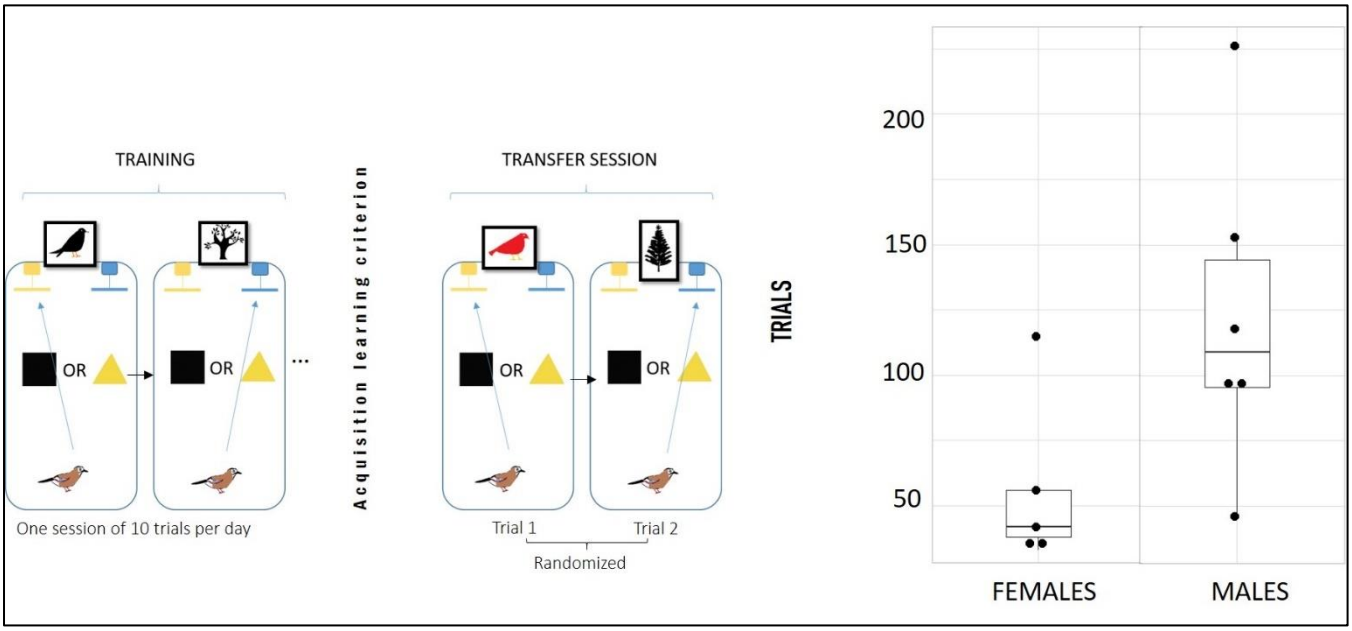

Figure 26 Discrimination task and transfer session. Design of the experiment and number of training trials until succeeding the transfer session in females and males.

Incidental encoding test:

The incidental encoding test is composed of three phases: two presentation phases and one test phase, realized the day after the jays passed the transfer session (Figure 27). During the first presentation phase, a contextual cue non-encountered before (e.g., a purple triangle) was placed on the wall or on the door of the testing compartment. Then, the jays were presented with a picture non-encountered before (e.g., unknown picture of bird) placed on

the Plexiglas window of the door of the testing compartment. The perches were not provided in the experimental compartment, so that the jays could not choose to land on the perch corresponding with the type of picture presented. The bird stayed in the present design for 5 minutes. Then, the picture and the contextual cue were removed, and the following phase started. During the second presentation phase, a contextual cue (e.g., blue circle), and a novel picture (e.g., picture of a tree if the bird was presented with the picture of a bird at the first phase) was presented. As during the first presentation phase, the perches were not provided inside the testing compartment. The bird stayed in the present design for 5 minutes. Then, the picture and the contextual cue were removed. The order of presentation of the two contextual cues (e.g., purple triangle and blue circle), of the two types of picture (e.g., bird or tree), as well as the association contextual cue-type of picture was counterbalanced across subjects (Figure 28).

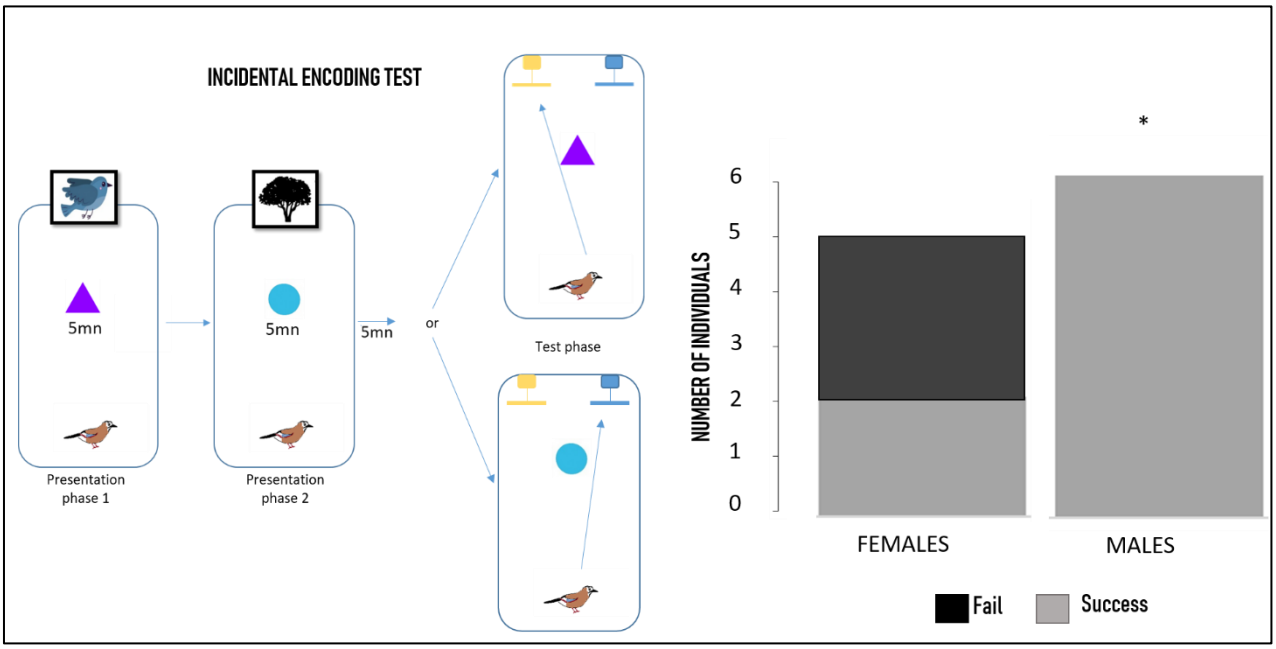

Figure 27 Incidental encoding test. Design of the experiment and number of individuals succeeding or not at test phase.

Five minutes after the end of the second presentation phase started the test phase. One of the contextual cues (e.g., purple triangle) presented during the presentation phases was placed back in the testing compartment. Contrary to the presentation phases, no bird/tree picture was presented, while the two perches were hanged so that the jays could choose to land on one of the two perches. If jays had incidentally encoded the contextual cues provided in the testing compartment during presentation phases (even though focusing on the contextual cue was previously irrelevant for succeeding the discrimination task), they

should be able to retrieve which type of picture was presented alongside this particular contextual cue, and land on the corresponding coloured perch. For example, if the purple triangle was presented alongside a picture of a bird during presentation phase 1 and the blue circle was presented alongside a picture of a tree during presentation phase 2, then at test phase, jays should land on the perch associated with the coloured portrait-oriented pictures of birds if the purple triangle is presented. The test was considered successful if the jays landed on the perch associated to the type of picture encountered previously with the same contextual cue (Figure 28). The jays performed the incidental encoding test only once, as the question would not be unexpected anymore after repeated exposure to the same paradigm. The contextual cue used during the test phase (i.e., the one encountered at the first or at the second presentation phase) was counterbalanced across subjects.

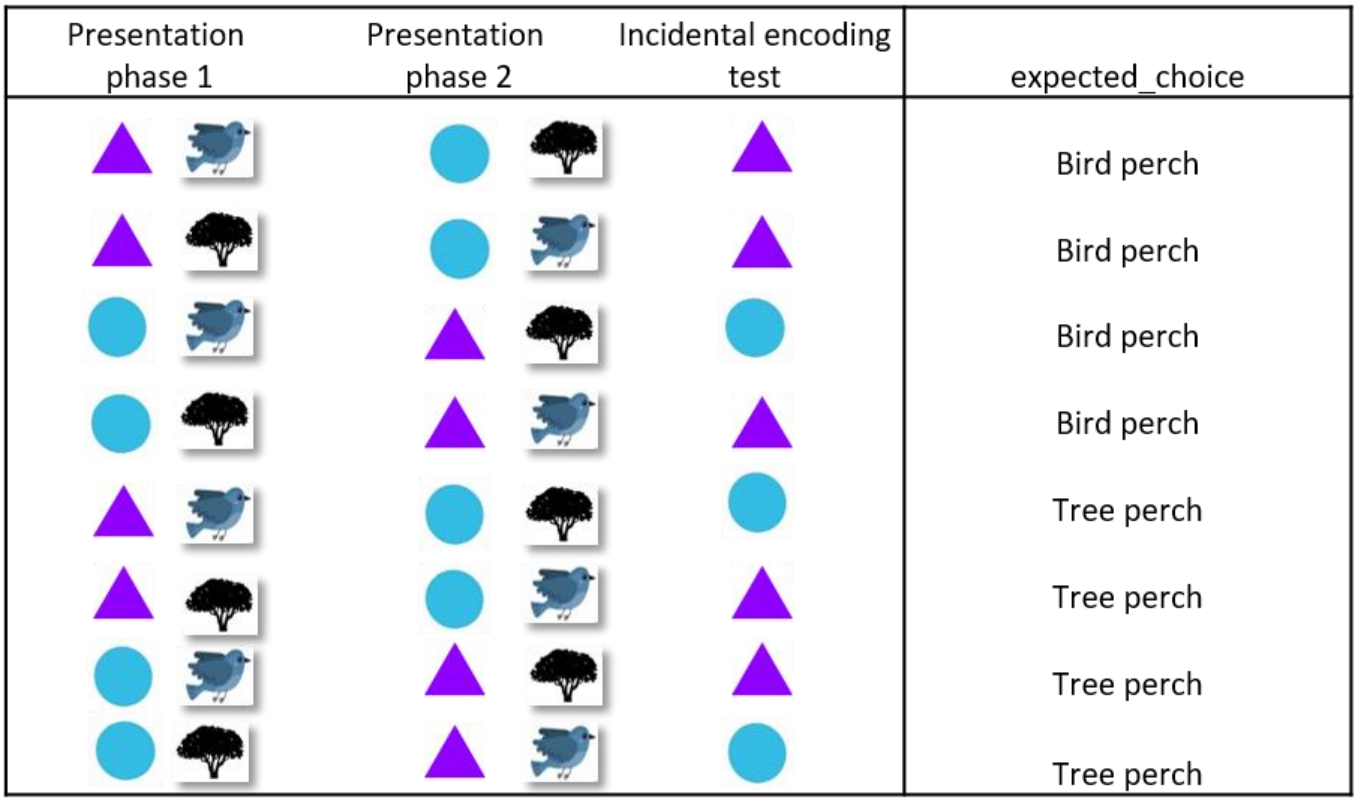

Figure 28 Complete design of the incidental encoding test.

e. Statistical analysis:

All data were computed using R software (version 3.5.1).

Discrimination task. As the data did not meet the assumption of normality, we used non-parametric tests. When data meet the assumption of homogeneity of variances, we used exact

Billard, P., Jozet-Alves, C., Clayton, N. S. (in revision in Animal Behavior and Cognition) A new paradigm for assessing discriminative learning and incidental encoding of task-irrelevant contextual cue in Eurasian jays.

permutation tests, and when it was not the case we used Wilcoxon signed-rank tests. To verify that birds learnt the discrimination task, we used a Wilcoxon test (wilcox.test function on R) to compare the scores (i.e., number of correct choices) obtained during the first and the last 15 trials of training. A perch choice was considered correct when a jay chose the perch associated with the type of picture presented. To compare the number of trials 1) to first reach the acquisition criterion, and 2) to succeed at a transfer session, between males and females, we used exact permutation tests.

Incidental encoding test. To test whether the majority of tested individuals choose the correct perch at test phase of the incidental encoding test, we used binomial tests. We considered that an individual succeeded the test when it chose the perch associated to the type of picture encountered previously with the same contextual cue. To test the effects of the order of picture presentation at phase 1 and 2 (i.e., birds might choose the perch associated to the last picture encountered independently of the contextual cue presented at test) and sex (male versus female) on the accuracy of responses (i.e., correct versus incorrect choice; dependent variable), we used the generalized linear models (GLMs) statistical method. GLMs handle non-normal data, conceding to specify different distributions, such as binomial. Moreover, GLMs allow to test the total variance of our data, without averaging the trials of individuals, as it is often done with classic analysis of variance. To investigate the contribution of each fixed effect (i.e., order and sex) and their interactions, we used the Anova function in R.

2. Results

a. Discrimination task and transfer sessions

Jays (n = 11) succeeded a transfer session after a median of 94 training trials (range: 33 – 226 trials; 42 training trials for females and 109 training trials for males). The number of correct choices significantly increased between the first and the last 15 trials of training (W = 5.5; $p <$ .001). Eight birds (five males and three females) passed the first transfer session with success, while two birds went through two transfer sessions to succeed (one male and one female), and one bird through three transfer sessions to succeed (one female). The median number of transfer session needed was 1.4. Females were significantly faster to reach the learning criterion the first time (p = 0.044, median number of trials: females = 38; males = 97). Females were also marginally faster to learn the discrimination rule (i.e., number of trials until succeeding a transfer session; p = .052, median number of trials: females = 42, males = 109; Figure 26).

b. Incidental encoding test

Billard, P., Jozet-Alves, C., Clayton, N. S. (in revision in Animal Behavior and Cognition) A new paradigm for assessing discriminative learning and incidental encoding of task-irrelevant contextual cue in Eurasian jays.

The number of jays succeeding the incidental encoding test was not significant when considering the whole group of tested birds (Binomial test: $p = .2$, Figure 27). However, when focussing separately on males and females, we found that the number of males succeeding the task was significantly higher than random (6 out of 6; $p < .05$) whereas this was not the case in females (only 2 females out of 5 chose the correct perch; $p = 1$; Figure 27). Our generalized linear model showed a significant effect of sex ($p < .05$) and no effect of order ($p = .71$) on accuracy during test phase (i.e., correct versus incorrect choices). The probability of succeeding is higher in males, and it is not dependent on the last type of picture encountered.

Billard, P., Jozet-Alves, C., Clayton, N. S. (in revision in Animal Behavior and Cognition) A new paradigm for assessing discriminative learning and incidental encoding of task-irrelevant contextual cue in Eurasian jays.

3. Discussion

Our results showed that all of the jays we tested were able to solve the discrimination task. Females were significantly faster than males to learn the discrimination task, namely the association between the three different pictures of each type and their corresponding perches, and females were marginally quicker to learn the discrimination rule (i.e., association between coloured portrait-oriented pictures of birds versus black-and-white landscape-oriented pictures of trees and their corresponding perches). All of the males (six out of six) that we tested passed the final incidental encoding test, but only some of the females we tested (two out of five) made the correct choice at the final incidental encoding test.

This study is the first to use a picture discrimination task with Eurasian jays. We here show that jays were able to perform a simple discrimination task by landing on a left or right coloured perch associated randomly with coloured pictures of birds oriented in portrait, and black-and-white pictures of trees oriented in landscape. In the literature, birds have been found to perform well on visual discrimination tasks (e.g., colours: Clayton and Krebs, 1994a; Range et al., 2006; Range et al., 2008; Miller et al., 2016a; Miller et al., 2016b; damaged or clear leafs: Real et al., 1984). Picture stimuli were also used to investigate object categorization and generalization in birds (e.g., Watanabe, 1997; Bovet and Vauclair, 2000; Spetch and Friedman, 2006; for a review on the role of picture in avian cognition see Weisman and Spetch, 2010). For instance, pigeons are able to discriminate pictures of paintings from different painters and show similar discrimination processes than those in humans (Watanabe, 2001), and to discriminate pictures of birds versus mammals (Cook et al., 2013). As the study of discriminative learning was not the main focus of our experiment, the different characteristics of the pictures -orientation (i.e., portrait and landscape), presence or absence of colours, and image of a tree or of a bird- were confounded to facilitate the learning of the discrimination task. In other words, we hypothesized that pictures differing in several characteristics would be easier to discriminate because the jays might be able to focus on one or the other characteristic (e.g., presence or absence of colours). Further studies are now needed to determine whether jays were able to conceptualize the difference between pictures of trees and birds, or whether they used other characteristics of the picture such as orientation or colouration to efficiently solve the task.

Although this result was not expected when our study was designed, our experiment showed that female jays were faster to reach the acquisition criterion of the discriminative task. Sex differences in cognitive abilities are well documented in literature; these differences can be

Billard, P., Jozet-Alves, C., Clayton, N. S. (in revision in Animal Behavior and Cognition) A new paradigm for assessing discriminative learning and incidental encoding of task-irrelevant contextual cue in Eurasian jays.

explained by the strategy used by individuals to solve a cognitive task rather than their learning abilities per se (Beiko et al. 2004). Behavioural research has shown the influence of sex and gonadal hormones on cognitive performance across various tasks and in a variety of species (e.g., rats: Luine and Dohanich, 2008; great tits: Hodgson et al., 2008; for a review on the influence of hormones in vocal behaviour in songbirds see Bottjer and Johnson, 1997; humans: Bell and Saucier, 2004). The increase in hormones specific to the breeding season (i.e., testosterone and oestrogen) is linked to sex differences notably in the use of spatial strategies. For instance, mated female pinyon jays are less accurate than males to retrieve food caches after long intervals (Dunlap et al., 2006, for reviews on sex differences in spatial ability see Jones et al., 2003). Sex differences in our study might be explained within an ecologically framework. Indeed, jays were tested during breeding season where changes induced by reproductive processes can be observed in males and females (Salvante and Vézina, 2010). During the breeding season, female birds reduce their activity to save energy, whereas males are more active due to an increase of testosterone, which enhances their territoriality and aggressive behaviour towards other males (e.g., Meddle et al., 2002). It remains here to be tested whether there is a seasonal variation in learning rates that could contribute to the sex difference observed in this discriminative task.

In our experiment, eight out of the eleven jays chose the correct perch during the final incidental encoding test. The choices made were not related to the order of presentation of the two types of pictures (i.e., during presentation phases 1 and 2), showing that jays were not systematically choosing the perch associated to the last encountered type of picture (i.e., encountered at presentation phase 2). Jays were then relying on the contextual cue presented at test, to retrieve which type of picture was previously seen with this same contextual cue (i.e., during either the first or second presentation phase). This suggests that jays incidentally encoded contextual cues during presentation phases. As contextual cue was previously non-relevant for the discrimination task, and as jays only went through the encoding test once, they did not know that the contextual cues encountered during presentation phases will be later useful. This procedure prevents jays to intentionally focus their attention on these cues at presentation phase and deliberately encode them for later use to obtain a reward. While our sample size was low, we found a significant effect of sex on the probability to succeed the task. All males passed the final incidental test with success (six out of six), whereas only two females out of five did so. As there was one chance out of two to choose the correct perch during the test, this suggests that the females made their decision completely at random. The results of this experiment

presented here suggest that female jays might focus on task-related elements only (i.e., pictures of birds and trees), while males might pay more attention to other, non-task relevant details (i.e., contextual cues). This could explain why females were faster to learn the discrimination task while not succeeding at incidental test, and on contrary, why males were slower to learn the discrimination task while succeeding at incidental test. As our sample size is low, it should be important to confirm this unexpected sex difference, and assess whether the breeding season plays a role in this cognitive dimorphism if confirmed.

There is good evidence that various animal species can recall what happened where and when on the basis of specific past events. However, it is impossible to tell whether this episodic-like memory for what happened where and when really is like episodic memory because there is no way of knowing whether animals' memory recollection is accompanied by the phenomenological elements of episodic memory, namely the projection of self in time (i.e., autonoetic awareness and chronesthesia). Incidental encoding is another crucial defining feature of episodic memory and can bring new insights about the question of whether non-human animals possess episodic cognition. Most of the tasks investigating incidental encoding in animals used the to-be-incidentally-encoded materials as part of the main task. Consequently, animals may have paid attention to these materials and encoded some of its features. Our study presents a new way of investigating incidental encoding in animals where the attention of the animal is not driven towards the to-be-incidentally encoded stimuli. On the contrary, animal's central focus is driven on a distractive simple discrimination task, and the incidental stimuli (i.e., the contextual cue) are totally irrelevant for this task. In the subsequent unexpected test, the jays were asked to remember and use this contextual cue to obtain a reward. It is possible that the jays associated the contextual cues with the picture even after a single exposure, and if so they could have solved the incidental encoding test through associative learning (i.e., association picture/contextual cue). However, the fact that jays had been exposed to non-relevant contextual cues during training, coupled with the single presentation of the new contextual cues during the presentation phases of the incidental encoding test and the unexpected aspect of the final test are key elements and ones designed to minimize an explanation in terms of associative learning. The crucial point was to distract the jays from the crucial elements that will be asked later, making sure that they did not focus their attention on it, and therefore allowing us to test their memory for incidental features.

To conclude, our study describes a simple novel procedure for testing discrimination learning in Eurasian jays. Furthermore, this study provides a new way to investigate incidental encoding

Billard, P., Jozet-Alves, C., Clayton, N. S. (in revision in Animal Behavior and Cognition) A new paradigm for assessing discriminative learning and incidental encoding of task-irrelevant contextual cue in Eurasian jays.

in animals where the to-be-incidentally encoded stimulus is not the centre of the attention of animals performing the task. It is hoped that such procedures might provide insightful knowledge towards a better understanding of the evolution of episodic cognition in non-human animals.

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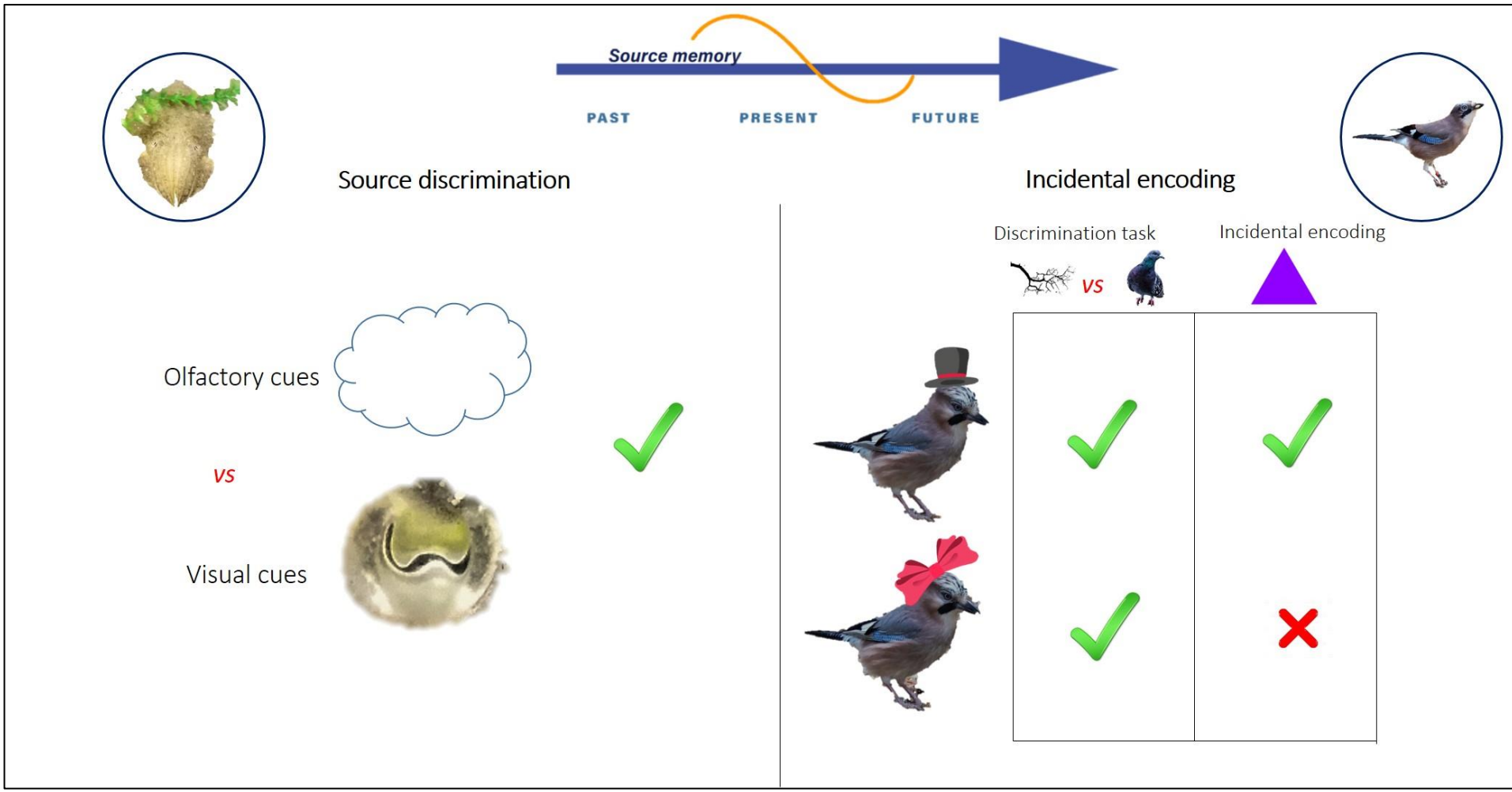
Source memory
PAST
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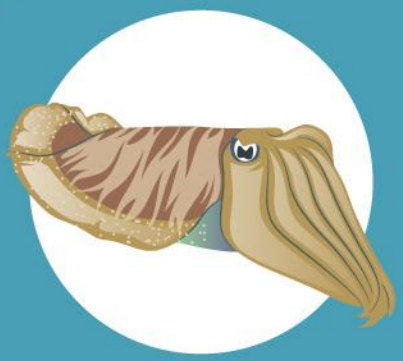
FUTURE
Source discrimination
Olfactory cues
vs
Visual cues
Incidental encoding
Discrimination task
vs
Incidental encoding

CHAPTER

3



EXPLORATION OF FUTURE-PLANNING

Article 3:
Billard, P., Schnell, A. K., Clayton, N. S., & Jozet-Alves, C. (2020). Cuttlefish show flexible and future-dependent foraging cognition.
Biology Letters, 16(2); 20190743. DOI: 0.1098/rsbl.2019.0743.

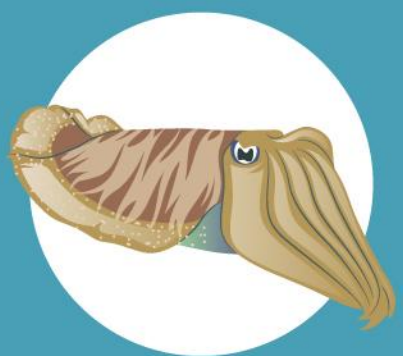
Preliminary study:
Poncet, L., Roig, A., Billard, P., Bellanger, C., Jozet-Alves, C. (preliminary study). Future-oriented behaviour in the common cuttlefish.

Introduction of Chapter 3

Increasing literature documents the role of episodic memory for anticipating the future (e.g. Schacter and Madore, 2016; Szpunar et al., 2014). Indeed, retrieving an episodic memory would support the construction of imagined future events. The ability to imagine future events based on previous experiences, would be allowed by the ability to reconstruct memories (as postulated by the constructive episodic simulation hypothesis; Schacter and Addis, 2007). Among the evidences for the role of episodic memory in future-oriented thinking, there is for instance the fact that similar neural networks are activated when remembering the past and anticipating the future (e.g. Klen, 2013; Schacter et al., 2012). Thus, investigating animal capacities to think ahead would bring further knowledge on episodic cognition: reconstructive processes and flexible use.

Article 3 / Part 1: Future-oriented behaviour:
In this first study, we investigated cuttlefish capacity to flexibly change their predatory behaviour according to different foraging conditions. When cuttlefish knew that they were going to have shrimp at night (their preferred food), they stopped eating crabs (their less preferred food) during the day. When they could not predict whether their preferred food would be available at night, they kept eating the crabs during the day. Finally, cuttlefish appeared able to flexibly adapt their foraging strategy on a day-to-day basis depending on near future conditions.

Preliminary study 1 / Part 2: Exploration of future-planning in the common cuttlefish: In this second study, we assessed cuttlefish capacity to plan for the future independently of their current motivational state. The goal of the study was to determine whether fully satiated cuttlefish go where food but no shelter is available, because they know that it will allow them to eat when they will be motivated to several hours later.



I. Future-oriented behaviour

Cuttlefish show flexible and future-dependent foraging cognition

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Abstract

Some animals optimize their foraging activity by learning and memorizing food availability, in terms of quantity and quality, and adapt their feeding behaviour accordingly. Here, we investigated whether cuttlefish flexibly adapt their foraging behaviour according to the availability of their preferred prey. In Experiment 1, cuttlefish switched from a selective to an opportunistic foraging strategy (or vice versa) when the availability of their preferred prey at night was predictable versus unpredictable. In Experiment 2, cuttlefish exhibited day-to-day foraging flexibility, in response to what will happen in the proximate future (i.e., preferred prey available on alternate nights). In Experiment 1, the number of crabs eaten during the day decreased when shrimp (i.e., preferred food) were predictably available at night, while the consumption of crabs during the day was maintained when shrimp availability was unpredictable. Cuttlefish quickly shifted from one strategy to the other, when experimental conditions were reversed. In Experiment 2, cuttlefish only reduced their consumption of crabs during the daytime when shrimps were predictably available the following night. Their daytime foraging behaviour appeared dependent on shrimps' future availability. Overall, cuttlefish can adopt dynamic and flexible foraging behaviours including selective, opportunistic and future-dependent strategies, in response to changing foraging conditions.

Keywords: Foraging cognition, future-dependent behaviour, flexibility, cephalopods

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Introduction

Natural habitats can vary in the distribution and abundance of food availability. Many animals can navigate these environmental variations by modifying their foraging behaviour in response to the quantity and quality of food available in their environment, as well as the presence of other predators and competitors (Abrams, 2010). When there is ample prey, predators show selective behaviour, selectively foraging on higher quality or preferred prey and disregarding other types of food. However, when prey abundance or variety is limited, predators might exhibit opportunistic foraging, pursuing quantity more than quality (Jaksić, 1989; Cooper et al., 1999). Some species use simple cognitive mechanisms to solve such foraging problems such as responding to an environmental cue, e.g., the amount of prey diminishing. Other animals optimize their foraging behaviour through more complex cognitive mechanisms, such as enhanced spatial memory, value-based decision-making and executive control (Rosati, 2017). For example, predators might need to memorize food availability, when it would be optimal to eat, and where it is located. If the availability of a resource is difficult to forecast, they may need to use previous encoded knowledge about prey availability and information in the present context to facilitate foraging decisions (e.g., when and where to hunt). This decision is made on the basis of a trade-off between the cost of catching prey (e.g., energy, risk-taking) and the rewards it will provide while taking into account the probability of failing (i.e., value-based decision-making). The capacity to optimize these foraging decisions is also influenced by the capacity to restrain inappropriate motor responses, which is defined as executive control, including both inhibitory control and self-control. A lack of executive control might result in a failed attempt to capture prey immediately when the best decision might have been to stay hidden until the prey draws nearer, and thus increasing the likelihood of a successful attack.

Cuttlefish, *Sepia officinalis*, are described as opportunistic predators and exhibit a high level of diet generalism—feeding on a range of crustaceans, gastropods, fishes and other cephalopods (Pinczon du Sel et al., 2000; Guerra, 2006). Despite having a generalized diet, cuttlefish have strong individual food preferences (Wells, 1958, 1962; Darmaillacq et al., 2004a). They possess a large central nervous system from hatching, facilitating the ability to learn from a young age. Previous research shows that they are able to modify their behaviour in response to several distinct environments, adopting suitable and flexible mating or hunting strategies (Sobrino et al., 2002). Moreover, cuttlefish are able to flexibly change their food preferences if their preferred prey is devalued (i.e., it is coated with a quinine-based solution making it bitter; Darmaillacq et al., 2004b), and can inhibit their predatory motor behaviour when prey are

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visually presented but unobtainable ('prawn-in-the-tube' procedure, Messenger, 1973; Chichery and Chichery, 1992; Agin et al., 1998; Dickel et al., 2000). Cuttlefish are also capable of remembering episodic-like information based on what happened, where, and when by adjusting their foraging behaviour in response to the delay of replenishment of different food types being available (Jozet-Alves et al., 2013). Previous research suggests that episodic-like memory is linked to more complex cognitive abilities such as flexible decision-making and future planning (Clayton et al., 2003b; Schacter et al., 2012).

In the present study, we investigate whether cuttlefish are capable of flexible decision-making by testing whether they can adjust their foraging behaviour in response to changing prey conditions. In Experiment 1 (conditions 1 and 2), we investigate whether cuttlefish are able to change their foraging behaviour in response to environmental variations (predictable availability of their preferred food item at night versus unpredictable availability), and more specifically switch between an opportunistic to a selective foraging strategy, and vice versa. In Experiment 2, we aim to test whether cuttlefish exhibit day-to-day flexible foraging in response to acquired knowledge about what will happen in the proximate future (availability of their preferred prey the following night).

1. Material and methods

a. Subjects

Twenty-nine sub-adult European common cuttlefish (*Sepia officinalis*) participated in this study, ranging from three to six months of age. All eggs were collected from the English Channel along the northern coast of France and the southern coast of England. Two populations of cuttlefish were used. The first population (N = 19) was reared at the CREC, Luc-sur-Mer, Calvados, France (49.31° N, 0.36° W). These cuttlefish were housed in individual grey plastic tanks (10 cm in diameter) with circulating natural seawater at a temperature of 15 ± 1°C and maintained under artificial light conditions (12L : 12D cycle). The second population (N = 10) was reared in the Marine Biological Laboratory, Woods Hole, USA (41.53° N, 70.67° W). Dorsal mantle lengths were measured (mean dorsal mantle length ± s.e.m. = 41.79 ± 1.04 mm; range = 29–58 mm). These subjects were also housed individually in plastic tanks, which were supplied with a constant flow of filtered seawater (approx. 10 l min−1), maintained under natural daylight conditions and at a temperature of 15–17°C. Prior to experimental trials, all cuttlefish were fed a mixed diet of food items ad libitum, including thawed frozen prawn, live grass shrimp (*Palaemonetes paludosus* and *Crangon crangon*), live gammarid shrimp

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(*Platorchestia platensis*) and juvenile live crabs (*Carcinus maenas* and *Hemigrapsus sanguineus*). Subjects were used in several non-invasive experiments and were housed for the remainder of their life cycle until they died following senescence.

i. Food preference

For each cuttlefish, tests were conducted to determine individual food preferences between crab and shrimp. Both prey items were presented at equidistance and simultaneously to the cuttlefish. Subjects were allowed to choose one prey item only. The first prey captured by the cuttlefish was considered to be their preferred prey. Cuttlefish were tested five times per day over a period of 5 days. All subjects showed a preference for shrimp.

b. Experimental procedures

i. Experiment 1: conditions 1 and 2

One crab was placed in each cuttlefish tank every morning. At the end of the day, we recorded whether each cuttlefish had eaten the crab, and all remaining crabs were removed from the tanks. In condition 1, one shrimp was placed in each cuttlefish tank every evening. In condition 2, one shrimp was placed in each cuttlefish tank at random. The availability or absence of the shrimp was determined by the experimenter using a random number generator (StatTrek.com). After 16 trials, we reversed the experimental conditions for cuttlefish tested in conditions 1 and 2 to assess whether cuttlefish were able to quickly and flexibility adapt their foraging strategy. In total, subjects received 16 trials in each condition (32 trials in total per individual). Trials were compacted in four blocks of four trials per condition (see electronic supplementary material, data).

ii. Experiment 2

Two crabs were placed in each cuttlefish tank every morning (because these cuttlefish were older and larger and therefore required more food) at the CREC and at the MBL. At the end of the day, the number of crabs eaten was recorded for each cuttlefish, and all remaining crabs were removed from the tanks. At the end of the day, cuttlefish were provided with two shrimp every second evening (i.e., one evening out of two). Cuttlefish were tested until they reached a learning criterion of eight correct choices out of 10 consecutive trials. A choice was considered correct when cuttlefish refrained from eating the crab when shrimp were available in the evening, and when cuttlefish ate the crab when shrimp were not available in the evening.

c. Statistical analysis

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All data were analysed with non-parametric tests and computed using R software (version 3.5.1). To test the consumption of crabs through time (i.e., blocks of four days), per condition (condition 1 versus 2), or per day for Experiment 2 (days with or without shrimp at night) we used non-parametric permutation test analyses of data from factorial experiments (aovperm function, permuco package; Frossard and Renaud, 2019). Effect sizes and confidence intervals were computed (see electronic supplementary material).

2. Results

In Experiment 1, cuttlefish tested in condition 1 (i.e., shrimp systematically provided every night), significantly lowered their consumption of crabs during the day over time, while cuttlefish tested in condition 2 (i.e., shrimp provided at random) relatively maintained their consumption of crabs over time. The consumption of crabs was significantly different between conditions 1 and 2 ($p < 0.001$; effect size = 22.359). The effect size conveys that the variability between conditions 1 and 2 is 22 times higher than variability observed within conditions; this demonstrates a strong effect of experimental conditions on crab consumption. Cuttlefish tested in conditions 1 and 2 flexibly modified their foraging strategies when experimental conditions were reversed; demonstrated by a significant interaction between time (i.e., four blocks of 4 days) and condition ($p = 0.030$; effect size = 3.201, Figure 29).

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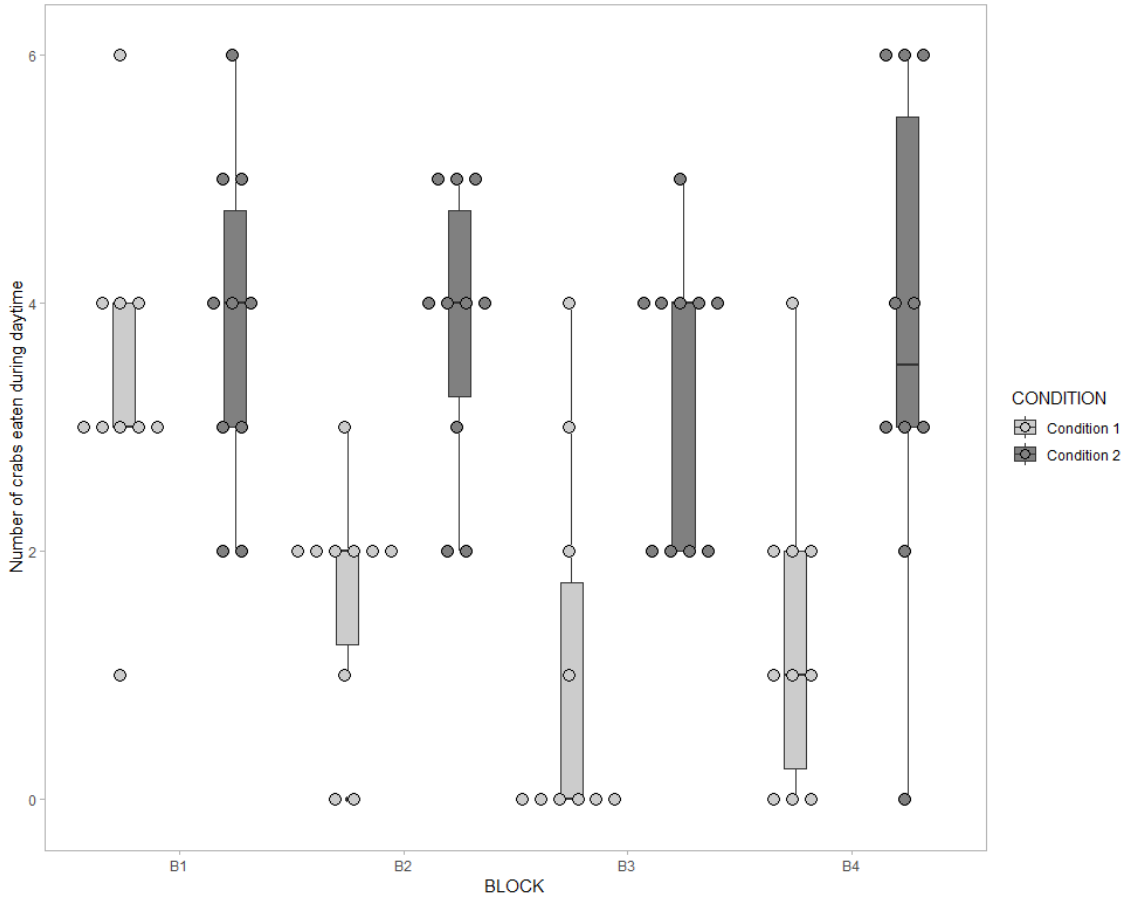

Figure 29 Consumption of crabs over time in conditions 1 and 2. Condition 1: consumption of crabs when shrimp were available every night. Condition 2: consumption of crabs when shrimp were only randomly available at night. The consumption of crabs significantly decreased over time in condition 1 while it was relatively stable over time in condition 2.

In Experiment 2, both cuttlefish from the CREC and from the MBL lowered their consumption of crabs during the day when shrimp were available the following night, while cuttlefish maintained their consumption of crabs during the day when no shrimp were available the following night (Figure 30). Statistical analyses showed no significant effect of time (i.e., four blocks of 4 days, CREC $p = 0.293$, effect size = 1.778; MBL $p = 0.707$, effect size = 0.144) but a significant effect of the conditions (i.e., days with or without shrimp at night, CREC $p = 0.005$, effect size = 10.449; MBL $p = 0.003$, effect size = 11.737), and a significant interaction between time and conditions (CREC $p = 0.001$, effect size = 16.514; MBL $p < 0.01$, effect size = 21.962). Effect sizes for conditions and interactions were greatly above 1 (from 10 to 21 times higher), indicating that cuttlefish alter their foraging behaviour in response to the availability of shrimps the following night, and that this behavioural alteration was even more pronounced across training. Cuttlefish tested in Experiment 2 reached the learning criterion (i.e., eight correct choices out of 10 consecutive trials) in 23 ± 12 trials at the CREC and 31 ± 6 trials at the MBL.

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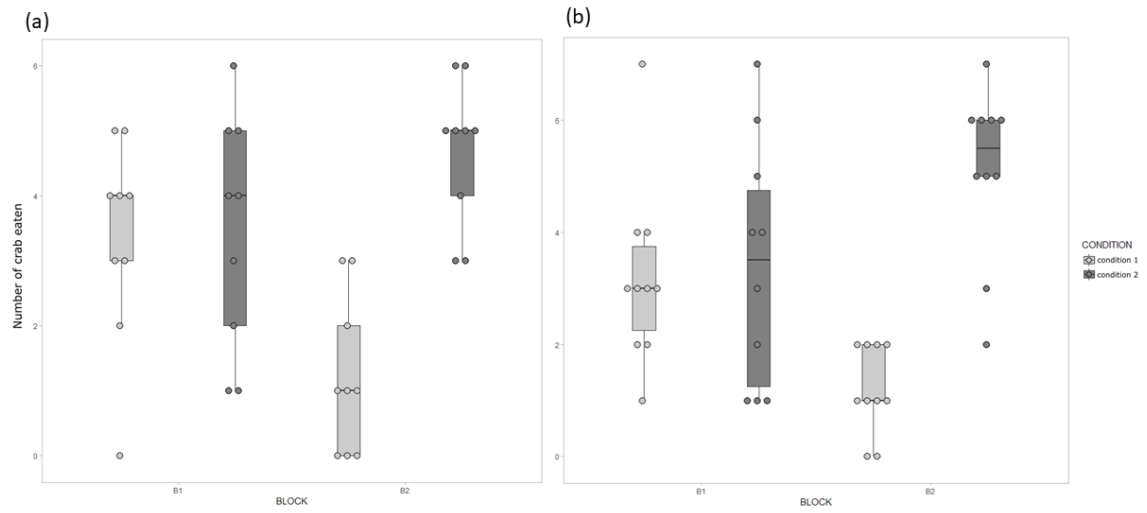

Figure 30 Consumption of crabs over time in Experiment 2 (i.e., shrimp were available on alternate nights). When shrimp were not available at night-time, the consumption of crabs remained stable over time in both laboratories. When shrimp were available at night-time, the consumption of crabs significantly decreased over time in both laboratories.

3. Discussion

Our study provides evidence of flexible predatory behaviour in cuttlefish. In condition 1, when one shrimp was available every evening, cuttlefish adopted selective foraging behaviour, significantly reducing their consumption of crabs during the day. By contrast, in condition 2, when shrimp were available randomly through time in the evening, cuttlefish adopted an opportunistic foraging strategy and maintained their consumption of crabs during the day. The random availability of shrimp in this condition meant that subjects were unable to predict the availability of their preferred prey and might adopt a 'less risky' option of consuming crabs. This increase in crab consumption might also be the consequence of lower food supply at night. When conditions 1 and 2 were reversed cuttlefish flexibly modified their foraging behaviour. Specifically, cuttlefish that were accustomed to eating crabs during the day significantly reduced their consumption, while those who were accustomed to waiting until the evening to eat shrimp begun eating crabs during the day. Theories on risk-managing and uncertainty postulate that animals must constantly adapt to changes (Dall, 2010). It has been argued that animals gather information about their proximate and distant background to reduce the

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uncertain outcomes of events, which is an adaptive mechanism for an organism (Dall and Johnstone, 2002; Dunlap and Stephens, 2016).

In Experiment 2, both groups from the CREC and the MBL adopted a flexible foraging strategy, adjusting the consumption of their less preferred prey in response to the upcoming availability of the preferred prey the following evening. Specifically, cuttlefish ate crabs when no shrimp were available in the evening but reduced their consumption of crabs when shrimp were available in the evening. This adjustment in crab consumption cannot be explained by their nutritional state as cuttlefish were consequently eating more crabs when they had access to shrimps the previous night, and vice versa. Our results could be explained in terms of positive and negative anticipatory contrasts (Cottone et al., 2008). Indeed, when cuttlefish know that they will not receive any shrimp at night, they would show a positive anticipatory contrast by eating the crabs during the day in anticipation of the absence of a later reward, but when cuttlefish know that shrimp will be distributed at night, they show a negative anticipatory contrast by refraining from eating the crabs, in anticipation of receiving a later reward. This pattern suggests that cuttlefish have rapid and flexible transient foraging strategies in response to changing environmental conditions, previous experience and potentially causal knowledge. Decision-making based on expected outcomes might have been modulated by knowledge of the causal structure of the environment (i.e., if my preferred food was not provided the previous night, I will have access to shrimp the following night).

But are the dynamic foraging patterns in cuttlefish driven by future-oriented behaviours or planning? According to the definition of future planning in animals (Clayton et al., 2003a), the observed behaviour must be flexible and sensitive to its consequences (e.g., Clayton et al., 2005). Our study shows that cuttlefish are capable of adjusting their foraging behaviour day-to-day in response to proximate-future environmental conditions (i.e., future-dependent foraging). Moreover, the decision they make during the day (i.e., the decision to eat the crabs or not) will likely have an impact on their later motivation to eat the shrimp in the evening. If cuttlefish decide to eat the crabs, then their motivation to eat the shrimp in the evening might be lowered, and they might 'miss' an opportunity to eat their preferred prey. However, at this stage, we cannot validate whether this future-dependent foraging behaviour observed in cuttlefish is underpinned by their ability to plan for the future. In order to determine whether cuttlefish foraging behaviour qualifies as future planning, we still need to test one critical criterion—are cuttlefish behaving independently of their current motivational state (i.e., desire to eat shrimps in the present moment)? Nevertheless, these results represent a promising way for further

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studies on flexibility and future-oriented behaviour in cephalopods. Given that cephalopods diverged from the vertebrate lineage approximately 550 million years ago, finding comparable future-oriented abilities in cuttlefish might provide valuable evolutionary insight into the origins of such a complex cognitive ability.

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II. Exploration of future-planning in the common cuttlefish

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Abstract

Some claim that animals cannot anticipate their future needs as they cannot escape their current motivational state. To challenge this hypothesis, we conducted an experiment on 16 captive-reared juveniles and 18 wild-caught adult cuttlefish. Each cuttlefish was tested in a Y-maze, where they were fed until satiety. Afterwards, they were proposed a choice between two arms: one with a shelter, but without any prey, and the other without a shelter but with a prey. They were confined inside the chosen arm overnight. During the night, cuttlefish which chose the arm with the shelter could not eat, whereas cuttlefish which chose the arm with food could eat and stay in the dark as artificial lighting is turned off at night. The following day, after being fed until satiety, the same choice test was performed. If cuttlefish were bound to their current needs (i.e., desire to escape from the light), they should choose the shelter arm. However, if they anticipated their future needs (i.e., hunger during the following night) irrespective of their current needs (i.e., hiding), they should prefer the arm with the food the second day. All cuttlefish but one went to the shelter arm the first day, a choice consistent with their current state of motivation. The second day, the shelter arm was not preferentially chosen anymore by juveniles and adults. A control test showed that cuttlefish are still attracted to the shelter. This suggests that the choice of the food arm the second day might not be the consequence of an associative learning between the choice of the shelter arm and a negative reinforcement (i.e., absence of food at night). Although the study presents some limitations and needs to be completed, it presents the first experimental procedure to investigate future-planning in a cephalopod.

Keywords: Future planning, episodic foresight, cuttlefish, cognition, episodic memory

Introduction

Episodic cognition is not only oriented towards the past. A growing literature argues that episodic memory's intrinsic function is to provide the ability to anticipate the future (e.g., Tulving, 1983, 2002, 2005; Suddendorf and Corballis, 1997; Atance and O'Neill 2001, 2005; Klein and Loftus 2002; Suddendrof and Busby, 2003; Michaelian et al., 2016). Evidence comes in part from neuroimaging and neuropsychological studies showing that both remembering a specific past event and projecting into the future activate the same neural networks (e.g., Okuda et al., 2003; Szpunar et al., 2007; Addis and Schacter, 2012). The function of episodic memory to plan for the future could be explained by its reconstructive nature (e.g., Wheeler and Gallo, 2010; da Silva and Lyra, 2020). Indeed, episodic memory is not considered as a literal picture of the past, it is rather considered as an active reconstruction. The flexible reactivation of the features composing several episodic memories would allow individuals to create/imagine future scenarios (e.g., Schacter and Addis, 2007).

Episodic memory has been described to develop progressively after early childhood in humans (e.g., Shing and Linderberg, 2011) and mature until adolescence (Wheeler and al., 1997; De Haan et al., 2006). Children, though able to remember information in a long-term manner (e.g., new-borns exhibit memory for their mother's face; Pascalis et al., 1995), have difficulties to manipulate time. Indeed, their memories might not be temporally organized (McCormack and Hoerl, 2001), and would mostly refer to semantic rather than episodic memory (Colombo and Hayne, 2010). Literature shows that future-planning also develops progressively after early childhood (Antance and O'Neill, 2005; Atance, 2008). Processing the future is not possible under the age of 5-years-old, because children cannot differentiate their current from their future needs (e.g., Atance and Meltzoff, 2005, 2006; Russel et al., 2010). For instance, studies showed that 4 and 5-years-old children were able to anticipate various situations whereas 3-year-old children presented more difficulties to project into the future (Suddendorf and Busby, 2005; Atance and Meltzoff, 2005). These behavioural difficulties for planning the future might be explained by the immaturity of the central nervous system in children and more particularly of the areas involved in episodic recall and planning (Ofen et al., 2007; DeMaster et al., 2014).

Mental time travel has long been considered as unique to humans (Roberts, 2002; Suddendorf and Corballis, 2007). More precisely, the Bischof-Köhler hypothesis states that animals are bound into the present because they are not able to act independently of their current

motivational state (Suddendorf and Corballis, 1997). To be considered as future planning, animal behaviour must answer to three behavioural criteria: its content, structure, and flexibility (Clayton et al., 2003a). The content of future planning refers to anticipating what will happen, where, and when on the basis of previous experience. The structure refers to the fact that the "where", the "when", and the "what" must be bound together in an integrated representation. Finally, the features composing the future episode must be flexibly reactivated and used. Crucial to future planning, animals must act for the future independently of their current motivational needs. For instance, if I am shopping for food while being hungry, it would not be a behavioural evidence for future planning, as I am acting in order to meet my current needs. On the contrary, if I am shopping for food while I am not hungry but in the anticipation of my next diner, it can be considered as a behavioural evidence of future planning. It remains here to state that all future-oriented planned behaviours in animals cannot be considered as future planning either. For instance, gathering food before hibernation, while sharing some features of prospective behaviours, does not necessarily involve learning and flexible use of past experience, as it might be innately driven.

Using described behavioural criteria to explore future planning in animals, several researchers have investigated whether future planning is or not a human distinctive feature (for reviews see Roberts, 2012; Templer and Hampton, 2013). Future planning was for instance investigated in rats (Wilson and Crystal, 2012; Crystal, 2012), primates (Mulcahy and Call, 2006; Osvath and Osvath, 2008; Beran et al., 2012), and jays (Correia et al., 2007). One striking example of future planning in animals is the "planning for breakfast" experiment of Raby and collaborators (2007). In this study, scrub-jays were trained in a three-room apparatus comprising a central compartment and one other compartment on each side (i.e., right and left compartments). In a first experiment, birds were given a breakfast with pine seeds in one of the compartment (e.g., left compartment) while no food was available in the other compartment (e.g., right compartment). At test, birds were pre-fed with pine seeds in the evening and then allowed to cache seeds in the three-room apparatus. Scrub-jays carried the seeds to the compartment where no food was available in the morning. In a second experiment, pine seeds were provided in one side compartment in the morning, and kibbles in the other compartment. At test, birds cached the seeds in the compartment where kibbles were available at breakfast, and they cached kibbles in the compartment where the seeds were available in the morning. These results showed that scrub-jays were able to determine whether they were going to receive

a breakfast or not in the morning in a specific compartment, and what type of food they were going to receive for breakfast, and plan for the future accordingly.

It has been shown that common cuttlefish (*Sepia officinalis*) possess the capacity to retrieve the past. For instance, they can retrieve which type of food was encountered, where, and how long ago (i.e., episodic-like memory, Jozet-Alves et al., 2013) and retrieve perceptive features of a previous event (i.e., source-memory, Billard et al., 2020a). In a recent study, we showed that cuttlefish can flexibly orient their predatory behaviour according to the future availability of their preferred food at night (i.e., Billard et al., 2020b). In this study, cuttlefish presented future-oriented behaviour because their day-to-day foraging behaviour flexibly changed depending on whether their preferred food will be available at night. However, authors could not control for cuttlefish current desire to eat their preferred food and they might have solved the task according to this current desire instead of planning. As cuttlefish have been shown to possess episodic-like features, and display future-oriented behaviour, they might be able to plan for the future independently of their current motivational state. This might be consistent with the hypothesis that episodic memory evolved to serve future planning (Klein et al. 2010).

This study aims to design an experiment allowing us to control the current motivational state of the cuttlefish in order to investigate their ability to plan for the future. As the areas involved in learning and memory of the cuttlefish brain develops mostly during the first three months after hatching (e.g., Dickel et al., 2000; Dickel et al., 2001; O'Brien et al., 2017), we decided to investigate future-planning ability in juvenile and adult cuttlefish. After being fed to satiety, juveniles and adults could choose between a shelter and a shrimp arm in a maze. The shelter arm answered to their current need to hide in the dark whereas the food arm answered to a future desire from shrimp. This choice was given to the cuttlefish two times in two days (one choice per day). We hypothesized that if cuttlefish are not able to plan for their future desire for shrimp, they would always choose the shelter arm. However, if cuttlefish were able to plan for the future, they should choose the shrimp arm.

1. Material and methods

a. Subjects

31 cuttlefish (*Sepia officinalis*) participated to this study.

- 13 juvenile cuttlefish between two and five months old were tested between September and December 2019. The eggs were collected in the English Channel, and the cuttlefish were hatched and were reared either in the Centre de Recherche en Environnement Côtier (CREC, Luc-sur-Mer, France; n=10) or in the aquarium of Nausicaa (Boulogne-sur-Mer, France; n=6) before being transferred to the CREC when they were around one month old. Cuttlefish were reared in group in plastic tanks (60x40x20cm) with circulating natural seawater at 17 ± 4°C, under natural light conditions. They were fed daily with live shrimps (*Crangon crangon*) and occasionally with crabs (*Carcinus maenas*) of suitable size.
- 18 adult cuttlefish were tested either in spring 2019 or in spring 2020. They were caught in the vicinity of Luc-sur-Mer using basket traps. Adult cuttlefish were subdivided in two groups: 10 adults were part of the experimental group, and 8 adults were part of the control group. Each individual was reared in an individual grey PVC tank (80x40x20cm) with circulating natural seawater at 15±1°C under artificial light conditions. They were fed daily with crabs (*Carcinus maenas*) and occasionally with live shrimp (*Crangon crangon*) of suitable size.

b. Apparatus

The apparatus was a white PVC Y-maze with circulating natural seawater at 15 ± 2°C under natural light conditions (Figure 31). The dimensions of each arm of the maze were 30x10x15cm, with 13cm of water. One arm was used as a start arm, while two arms were used as goal arms (i.e., food and shelter arms). Each arm could be closed by an opaque sliding plastic door. The end of each arm was partially covered by an opaque sliding PVC top to reduce the amount of light in the maze and thus attenuate the stress of tested cuttlefish. On day 1 and 2, a plastic shelter (grey PVC) with a plastic algae and a small rock were placed in one arm (the shelter arm) and a glass tube with three shrimps was placed in the other arm (the food arm). On day 3, the food arm was empty.

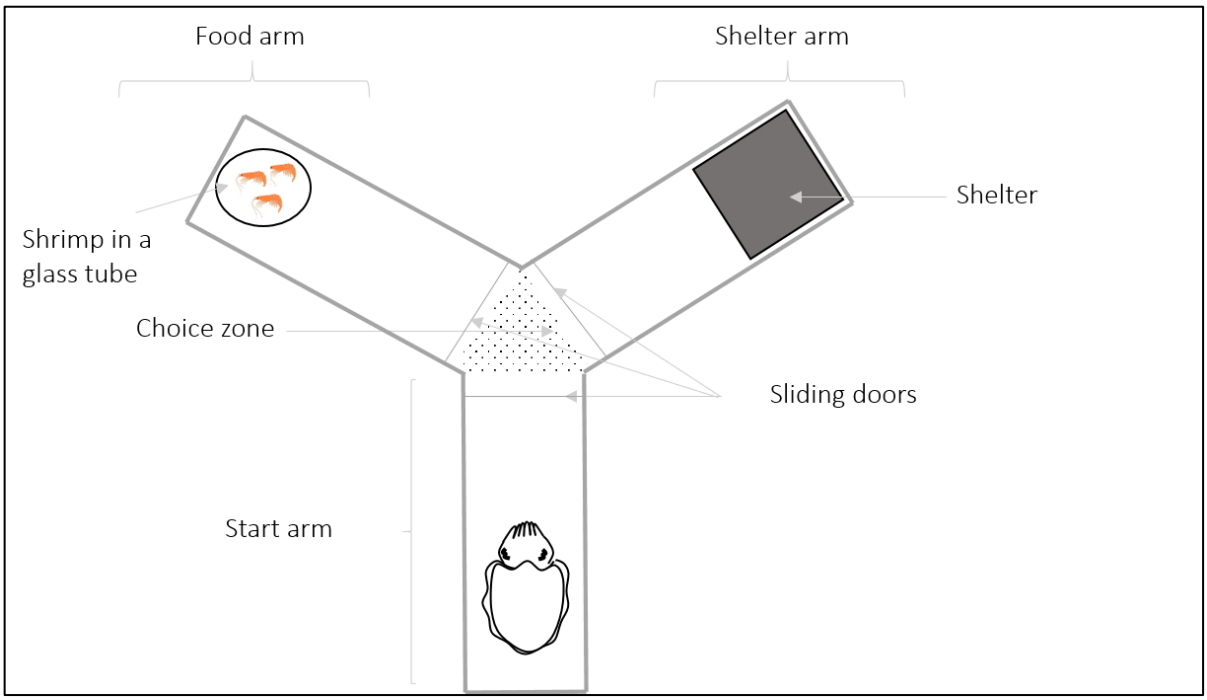


Figure 31 Y-maze used during the future-planning experiment.

c. Procedure

The acclimation (Figure 32) started in the morning and lasted a minimum of 24 hours and up to 3 days (until cuttlefish started to eat in front of the experimenter). During acclimation, cuttlefish could freely swim in all arms of the maze, and were fed with live shrimps (*Crangon crangon*, 3-4 of suitable size per day).

i. Day 1 / Experience phase:

In the morning, the arm of the maze where the cuttlefish was resting was closed with a plastic door, making this arm the start arm of the experience phase. The two other arms were

then prepared to be the shelter and the food arms according to the description presented above. Their left/right positions were randomly determined. The cuttlefish was then fed to satiety with shrimps, by placing a new shrimp each time one was caught and eaten. The criterion of satiety was reached when a shrimp left in the arm with the cuttlefish was not eaten during the following 30 minutes. Then, the shrimp was removed, and the sliding door was opened. The cuttlefish was allowed to move freely out of the start arm and to choose one of the two goal arms.

When the cuttlefish chose to enter an arm, the entrance was blocked off by sliding a plastic door. The cuttlefish stayed in this arm until the following day.

Experimental group: If cuttlefish from the experimental group chose the food arm, the glass tube was removed to free the shrimps inside this arm, allowing cuttlefish to prey upon them later. Consequently, during the following night, cuttlefish which chose the arm with the shelter could not eat, while cuttlefish which chose the arm with food could eat and stay in the dark as artificial lighting is turned off at night (Figure 32).

Control group: The procedure was exactly similar except that shrimps were delivered in both arms. Thus, if cuttlefish from the control group chose the shelter arm, they also received shrimps they could eat over the night (Figure 33).

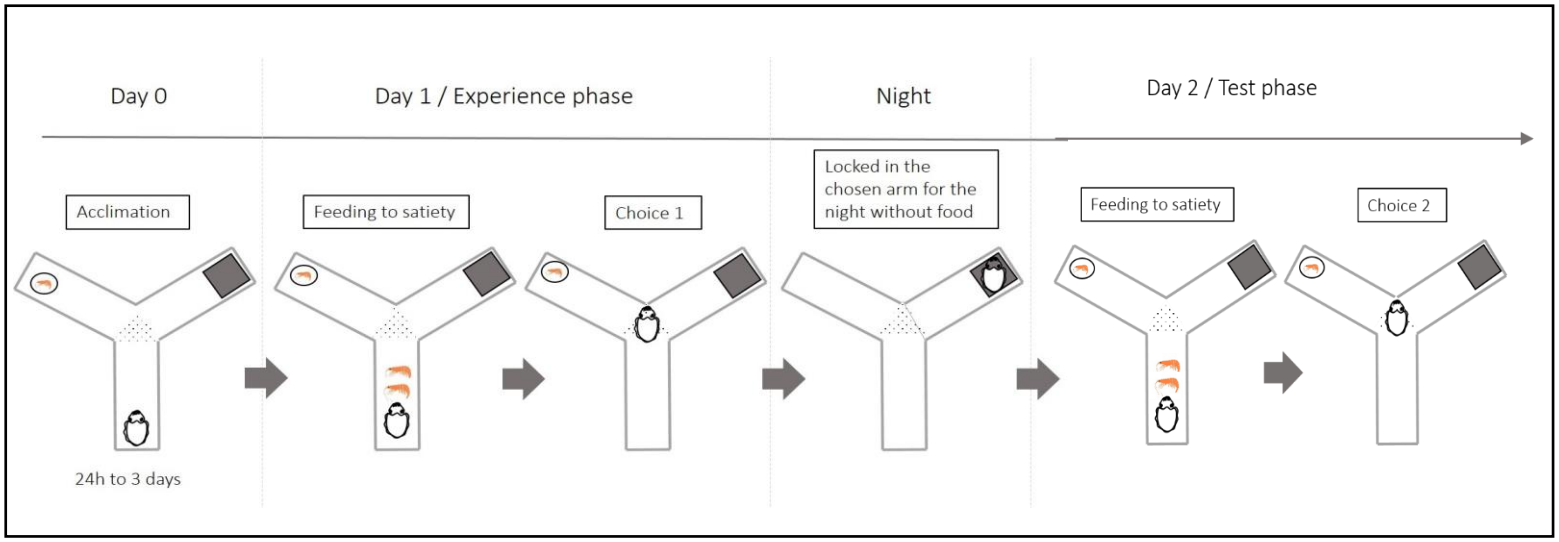


Figure 32 Procedure followed during the experiment for the test group.

ii. Day 2 / Test phase:

In the following morning, the procedure was conducted exactly the same way as day 1, except that: 1) the arm chosen at day 1 became the start arm for test phase; 2) if the cuttlefish

chose the shelter arm the previous day, all the elements of shelter were removed before starting the test.

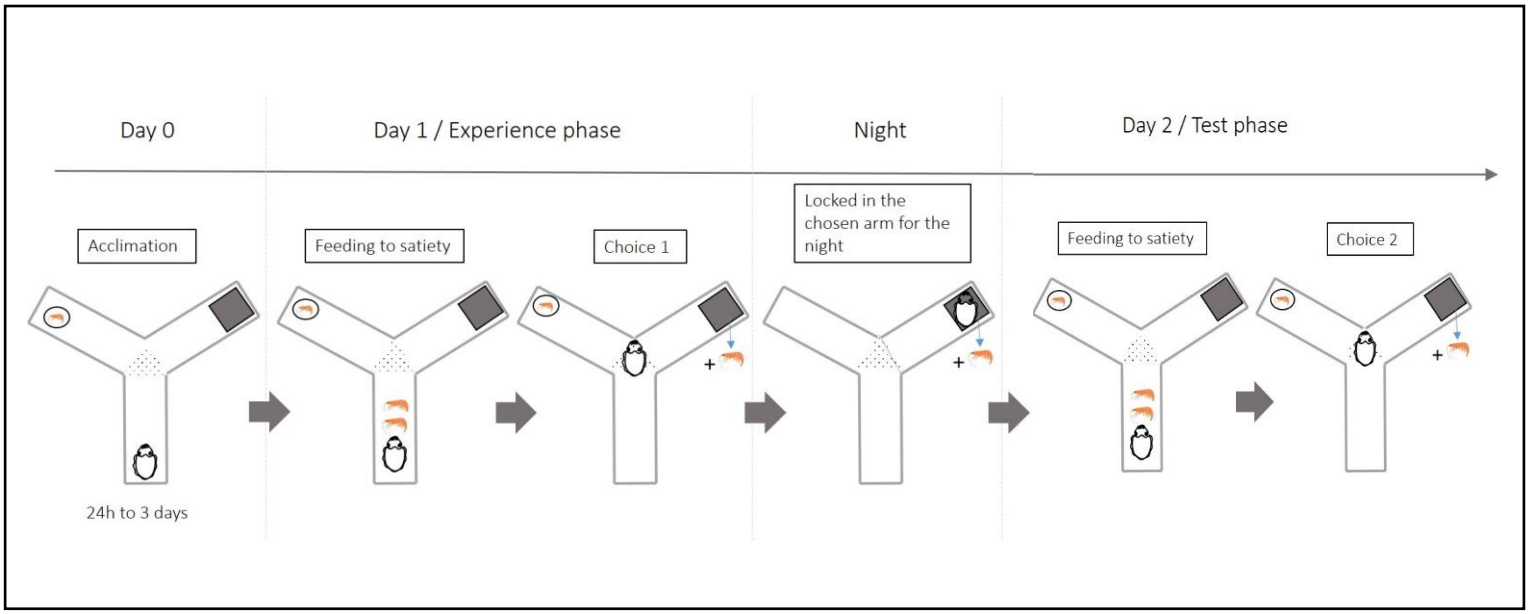


Figure 33 Procedure followed during the experiment for the control group.

iii. Day 3 / Control for shelter attractiveness (Figure 34):

The procedure was done the same way as in day 2, except 1) that the cuttlefish were offered to choose between a shelter arm and an empty arm (i.e., devoid of shelter or food); 2) that the experiment ended when one of the two arms was chosen.

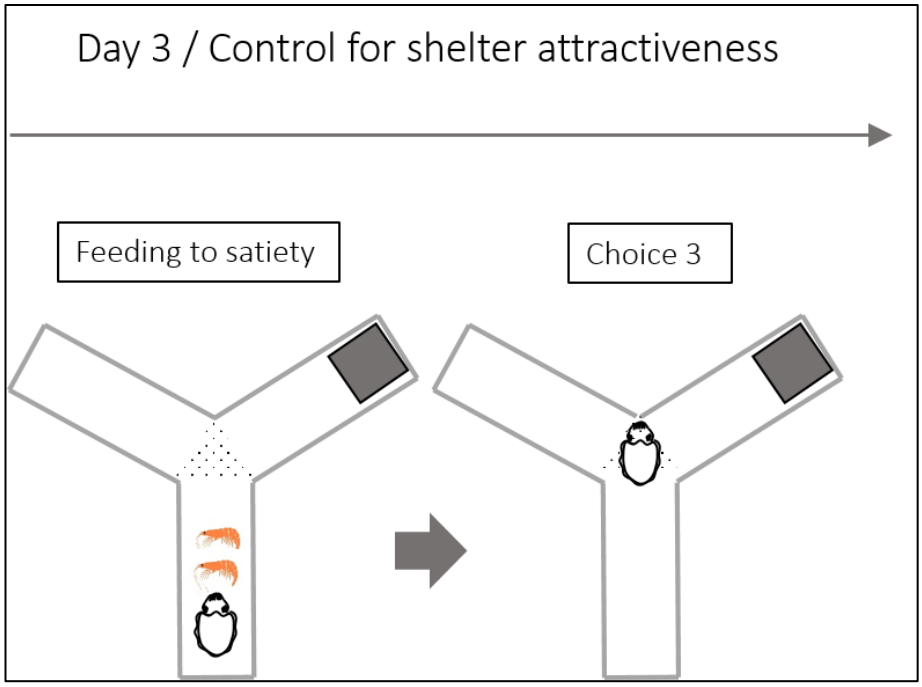


Figure 34 Procedure for day 3 / Control for shelter non-avoidance.

d. Video analysis

All choices were recorded with a SONY® HDR-CX240E Handycam and were analysed with Solomon coder beta 19.08.02. (copyright 2019 by András Péter; https://solomoncoder.com/).

The latency to choose was measured from the moment the cuttlefish eyes reached the "choice zone" (see Figure 31) and until the tip of the mantle exited it.

e. Statistical analysis

All data were analysed with non-parametric tests and computed using R software (version 3.5.1).

To test whether the shelter or the food arm was chosen by most cuttlefish, we used exact binomial tests (binom.test function on R) on day 1 and day 2 for each group.

To compare frequencies of shelter or food arm choices between the control group and the experimental group in adults, we used two Fisher exact tests, one at day 1 and one at day 2. We also used Fisher exact tests to compare frequencies of choices between juveniles and adults (experimental group) at day 1 and at day 2.

To test whether each individual (i.e., juveniles and adults) significantly changed the arm chosen between day 1 and day 2 we used Mc Nemar comparisons.

f. 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. Results

Results are summarized in figure 35.

Day 1

Binomial tests showed that at day 1, the shelter arm was chosen significantly more than the food arm in all groups: juveniles (11 cuttlefish out of 13 chose the shelter arm, p = .02, confidence interval: 0.55-0.98), adults from the experimental group (10 out of 10 individuals chose the shelter arm, p = .002, confidence interval: 0-0.31), and adults from the control group (8 out of 8 cuttlefish chose the shelter arm, p = .008, confidence interval: 0-0.37).

We did not find any difference concerning the frequency of shelter arm choice between juveniles and adults from the experimental group (p = .48, confidence interval: 0.14-Inf), and between the adults of the experimental and the control groups (p = 1).

Day 2

A preferential choice of the shelter arm was not shown at day 2 in both juveniles (10 cuttlefish out of 13 chose the shelter arm, p = .09, confidence interval: 0.46-0.95) and adults from the experimental group (6 individuals out of 10 chose the shelter arm, p = .75, confidence interval: 0.122-0.738). However, adults from the control group still chose the shelter arm significantly more at day 2 (8 out of 8 cuttlefish chose the shelter arm, p = .008, confidence interval: 0-0.37).

McNemar comparisons did not show any significant difference in the frequency of shelter arm choice between day 1 and day 2 in juveniles (p = .84, Q = 0.04, Figure 26), and adults from the experimental group (p = .12, Q = 2.45) and the control group (p = 1, Q = 0).

We did not find any difference concerning the frequency of shelter arm choice between juveniles and adults from the experimental group (p = .65, confidence interval: 0.049-3.85). However, Fisher F comparisons revealed a marginal difference in the frequency of shelter arm choice between the experimental group and the control groups at day 2 (p = .091, confidence interval: 0-1.663).

Day 3

All cuttlefish chose significantly more the shelter arm than the food arm. (juveniles, 11 out of 13 individuals, binomial test: p = .02, confidence interval: 0.55-0.98; adults from the experimental group, 9 out of 9 individuals, binomial test: p = .004, confidence interval: 0.664-1; adults from the control group, 6 out of 6 individuals, binomial test: p = .03, confidence interval: 0.541-1).

One adult cuttlefish from the experimental group and two cuttlefish from the control group were not tested at day 3 due to signs of senescence.

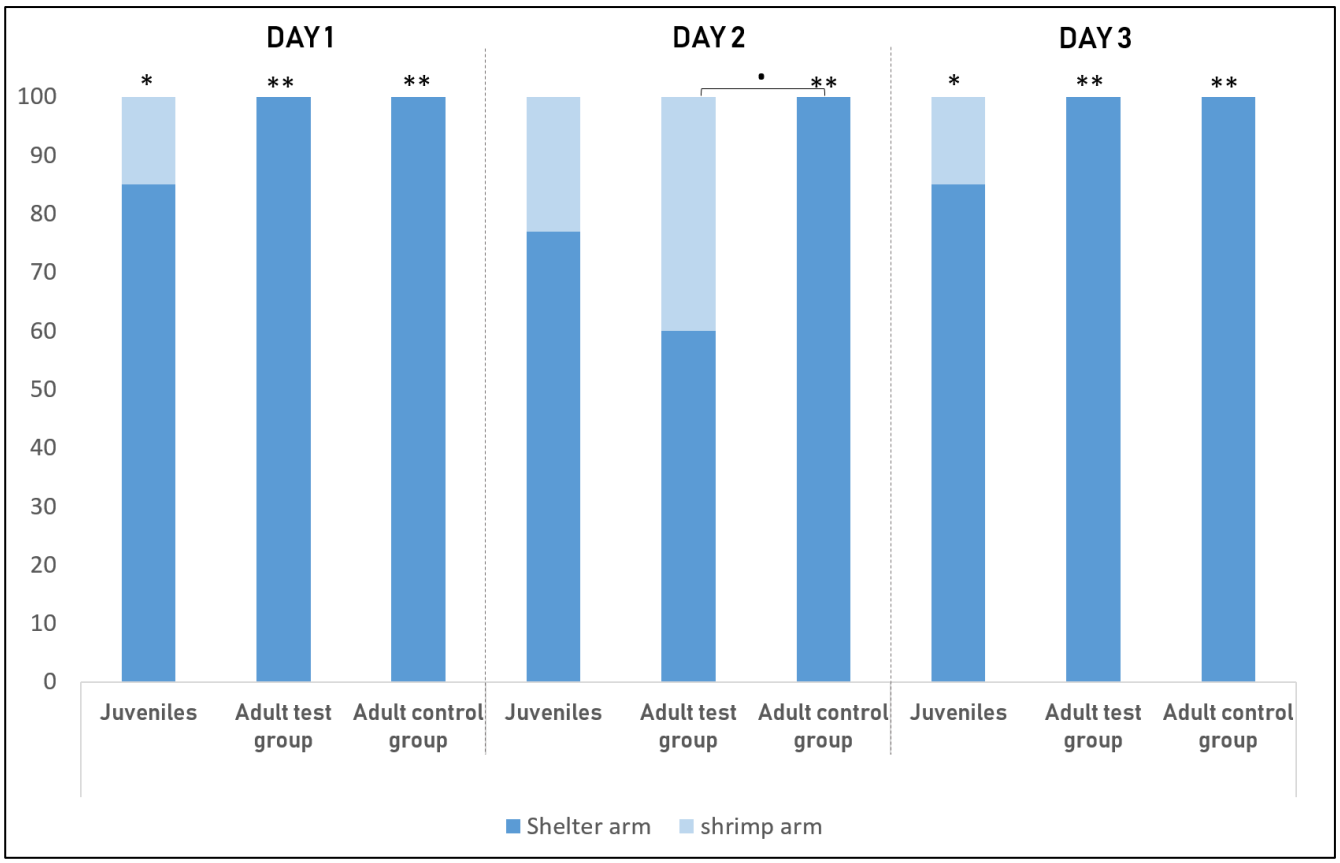


*Figure 35 Percentage of cuttlefish choosing either the shelter or the food arm at day 1, day 2, and day 3 for the juveniles, and the adults from the experimental and the control groups. Fisher exact test: p=.09; Binomial tests: p<.05 = *; p<.01 = ***

3. Discussion

Our study shows that in all groups of tested cuttlefish (i.e., juveniles and adults from both experimental and control groups) cuttlefish preferentially chose the shelter arm than in the food arm on day 1. On day 2, this preferential choice was not significant anymore for both juveniles and adults from the experimental group. We also found a marginal difference between the experimental group and the control group on day 2: adults from the control group kept going exclusively to the shelter arm the second day contrary to the experimental group. We did not find any difference between the juveniles' and adults' (test group) choices at day 2. On day 3, all the cuttlefish chose to go to the shelter arm.

All groups of cuttlefish initially preferred to go to the shelter arm, showing that cuttlefish are strongly attracted by the shelter. Indeed, cuttlefish are known to avoid open and lit areas when they cannot burry in the sand. Other studies have based their experimental procedures on this strong attraction for shadow (Alves et al., 2007; Jozet-Alves et al., 2008; Cartron et al., 2012). In these studies, shelter was used as a positive reinforcement for spatial learning. In our study, the choice of the shelter arm on day 1 answered the current need of the cuttlefish. Indeed, they were fed until satiety before running the choice test, so their current desire was to hide and not to eat, this then has driven their choice. A choice of the food arm was not expected the first day of testing. Indeed, cuttlefish did not know at this stage that choosing one of the two arms will make them locked inside overnight without being able to go to the other arm.

At day 2, in adults, the shelter arm was not preferentially chosen anymore in the experimental group, while it stayed preferentially chosen in the control group. When experimental cuttlefish chose the shelter arm at day 1, they were locked inside during the night without food. Our hypothesis was that cuttlefish would be able to learn that when they choose the shelter arm, they do not have access to the shrimp seen in the other arm. Consequently, we hypothesized that they would be less likely to choose the shelter arm (i.e., current need) at day 2, but rather choose to go into the food arm (i.e., future need). Our results seem to go in this direction as adult cuttlefish from the experiment group did not choose the shelter arm at day 2 as frequently as they did on day 1. The choice of the food arm on day 2 seems not to be explained by an avoidance of the shelter arm by the cuttlefish, which might have associated the choice of the shelter arm at day 1 and the absence of food during the night (i.e., negative reinforcement). Indeed, cuttlefish preferentially chose the shelter arm again at day 3, when cuttlefish have the choice between a shelter arm and an empty arm (i.e., no shrimp available). As the choice offered

to the cuttlefish is binary and might be erratic, it was important to compare the results obtained in the experimental group with results of a control group. In this control group, cuttlefish did not have to face a conflict at day 2 between a current need (i.e., need for a shelter) and a future ened (i.e., need for food), as shrimp were provided at night to the cuttlefish which have chosen the shelter arm at day 1. Contrary to experimental group, the control group consistently chose the shelter arm at day 2. This corroborates the hypothesis that when some cuttlefish in the experimental group chose to go into the food arm, it is unlikely due to a random choice. Choosing the shelter arm at day 2 might then be indicative of a future-oriented behaviour, suggesting that cuttlefish are acting independently of their current need. Some cuttlefish still chose the shelter arm at day 2. This choice does not mean that cuttlefish are not able to plan for the future, but it might indicate that the need to satisfy their current desire to hide is higher than their future motivation to eat at night. Indeed, cuttlefish are usually fed once a day, so some of them might not have been hungry during the night following day 1 (no future need to eat).

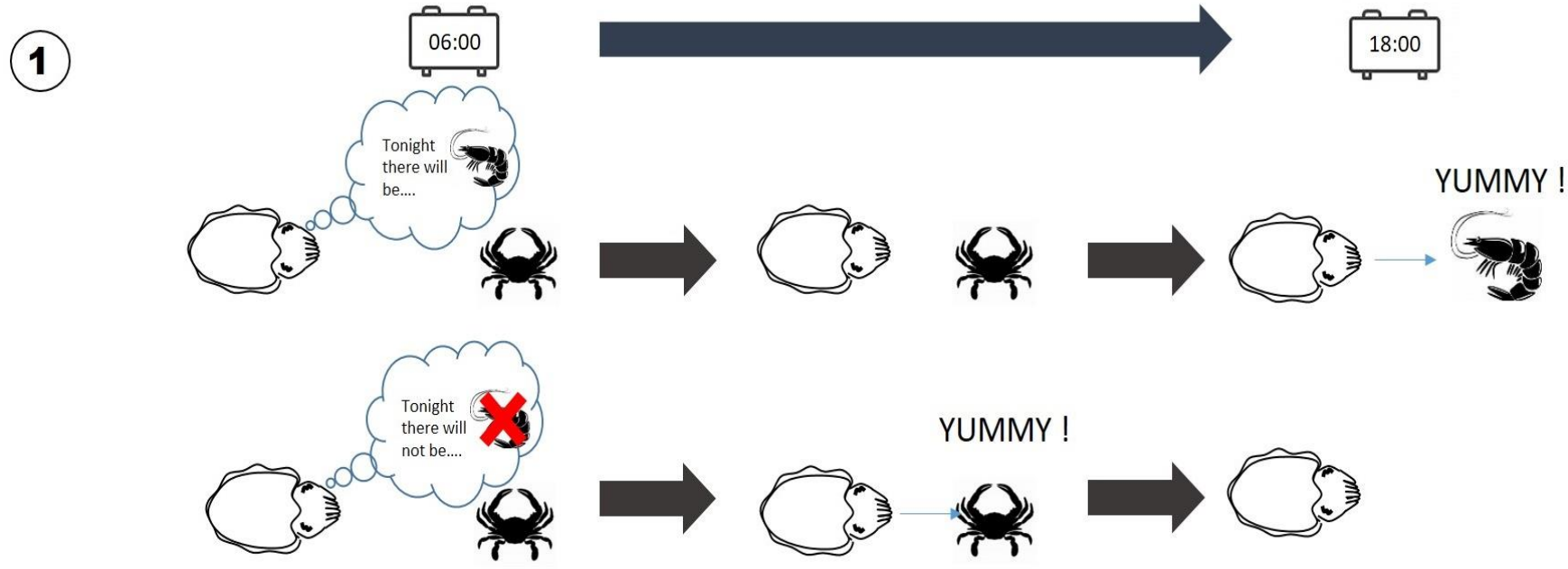
Contrary to what was expected, juveniles did not perform significantly lower than adults. As adults, juveniles did not preferentially choose the shelter arm at day 2. However, this arm was still chosen by 80% of the juveniles and we can wonder whether the 20% choices to the food arm was due to random or to planning. One major limitation of the study is the lack of control group to ensure that juveniles were not choosing randomly and that their behaviour at day 2 was due to their experience in the shelter arm during the previous night. These 20% of individuals choosing the food arm at day 2 might also be due to the variation in age of the juvenile group (2-5 months old) studied. Indeed, as the central nervous system is developing during the three months after hatching it is possible that some individuals possessed more developed capacities to plan for the future than others. Thus, it would be important to complete this study with a more homogeneous group of juveniles and to add a control group to compare the results of these juveniles.

Our study is the first to provide an experimental procedure to investigate future planning in cephalopods, controlling that cuttlefish are acting independently of their current needs. A recent study demonstrated future-dependent behaviour in cuttlefish (Billard et al., 2020b). The authors showed that cuttlefish were able to flexibly adapt their day-to-day predatory behaviour according to different experimental conditions and to the future availability of their preferred food. Other studies suggested that cephalopods might display future-oriented behaviour. For instance, octopuses were observed carrying coconut shells around as mobile dens to protect themselves from predators (Finn et al., 2009). However, it might be interpreted as a behaviour

undertaken to answer to a current need (Schnell and Clayton, 2019). Contrary to these previous findings, we designed an experiment allowing us to control the current motivational state of the cuttlefish in order to investigate their ability to plan for the future. Cuttlefish were fed until satiety before having the opportunity to make the choice between the shelter and the food arm. Thus, at day 2, when cuttlefish chose the food arm over the shelter arm they did so independently of their current needs to hide. These results provide the first evidence for future-planning in cuttlefish, bringing new data on mental time travel abilities in a cephalopod.

Future-planning is deeply rooted in episodic cognition and requires the validation of three criteria to be considered as such (i.e., content, structure, and flexibility, Clayton et al., 2003a). According to the literature, future planning would be possible if 1) the individual is able to retrieve the specific features composing a past event and 2) use it flexibly to construct a mental representation of a future event (Schacter and Addis, 2007). In our study, cuttlefish used their past experience of the absence of food during the first night to take a decision in the present (i.e., choice for the food arm at day 2), according to their future desire for shrimp during the second night. Thus, cuttlefish encoded and retrieved their past experiences in order to use it to plan the future. These results complete findings in terms of source-memory (Billard et al., 2020a) and future-dependent behaviour (Billard et al., 2020b) in cuttlefish, providing the first result on a possible anticipation independent of current motivational state in a cephalopod. Moreover, the fact that cuttlefish would possess both episodic memory and future-planning abilities suggests that these abilities might be tightly related and rely on similar cognitive mechanisms as it has been postulated in humans (e.g., Atance and O'Neill, 2001, 2005; Addis and Shacter, 2007).

To conclude, our study provides the first controlled procedure to investigate future planning in a cephalopod species. Our results showed that some juvenile and adult cuttlefish were able to anticipate their future need (i.e., desire for shrimp at night) independently of their current motivational state. Contrary to our expectations, juveniles and adults did not differ in their capacity to anticipate the future. This preliminary study needs to be completed (i.e., add a control group for juveniles and control their age to have a more homogeneous group) to bring valuable data on future-planning in cuttlefish, which would increase scientific knowledge on how episodic cognition is shared among species and how it has evolved under different environmental constraints.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YUMMY !
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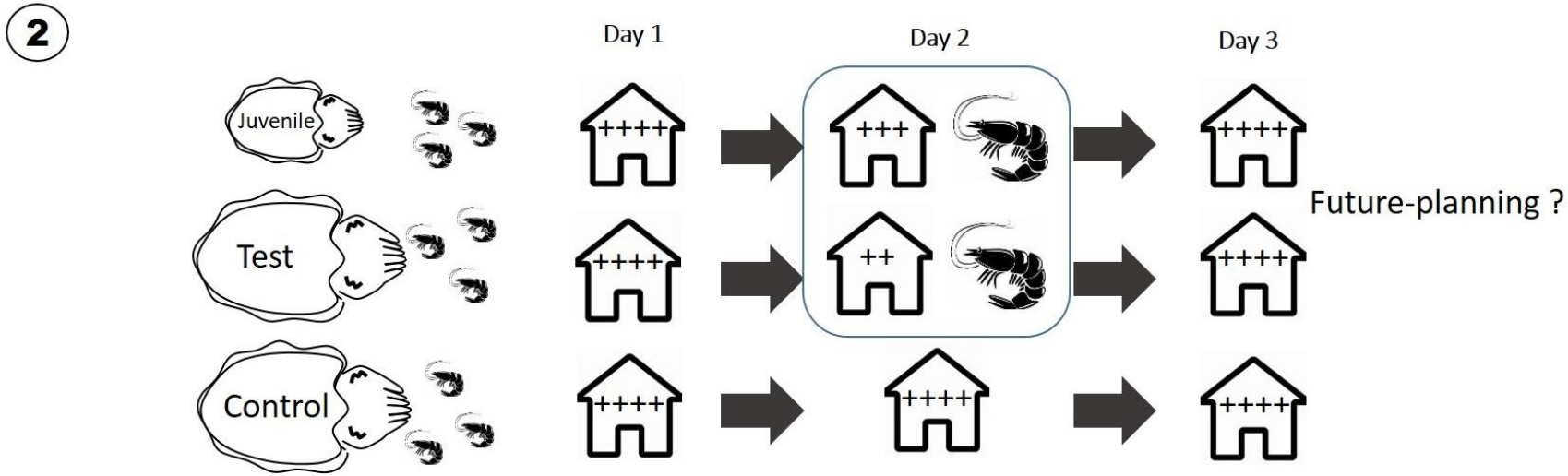
2
Day 1
Day 2
Day 3
Juvenile
Test
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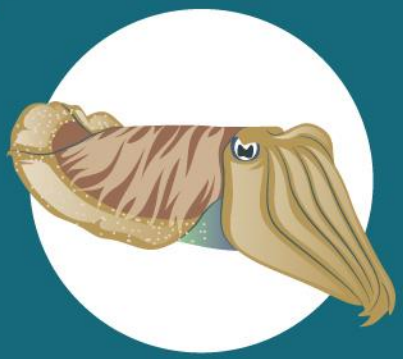
Future-planning ?

CHAPTER

4



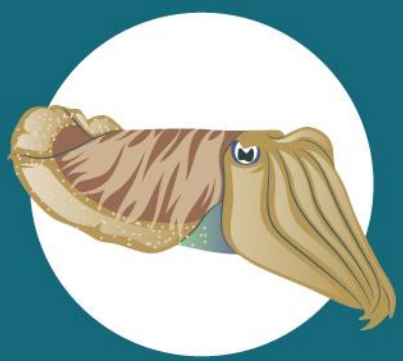
NEURONAL SUBSTRATES OF EPISODIC-LIKE MEMORY IN CUTTLEFISH

Preliminary study 2:
Billard, P., Schnell, A., Clayton, N. S., Darmaillacq, A. S., Jozet-Alves, C. (in preparation) Neuronal substrates of episodic-like memory in cuttlefish.

Introduction of Chapter 4

Preliminary study 2: Neuronal substrates of episodic-like memory in cuttlefish:

In this chapter, we will focus on the neural substrates of episodic-like memory in cuttlefish. Episodic-like memory has been widely studied in animals, and an increasing number of experiments support the idea that animals can project into the past. To date, the neural substrates of episodic-like memory have been studied in mammals, and especially rodents. The investigation of the neural substrates of episodic-like memory in cuttlefish would enrich our knowledge of episodic cognition in animals. As cuttlefish possess markedly different brain structures than vertebrates, it would be informative to better understand the neural pre-requisites of episodic cognition abilities, and improve our knowledge on how episodic cognition has evolved. In our study, ubiquitin-c terminal hydrolase (shown to be an immediate early gene in Aplysia) immunoreactivity (using custom-made antibodies) was studied in the brain of cuttlefish either involved in an episodic-like memory task or in the brain of control cuttlefish (exposed to the same motor and sensory stimulations than trained cuttlefish).



Neuronal substrates of episodic-like memory in cuttlefish

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Abstract:

Episodic-like memory experiments have provided behavioural evidence for animal's ability to remember what was encountered, when and where it was previously encountered, from vertebrates to invertebrates. Most studies focussing on neuronal substrates of episodic-like memory have been realized in rodents, and aimed at gaining a better understanding of the impairments of episodic memory observed during aging in humans. However, exploring the neural substrates of episodic cognition in an evolutionary framework might be useful to better understand why and how episodic cognition has evolved. Cuttlefish seems like a promising species for this, as it possesses markedly different brain structures than vertebrates and as it is the only invertebrate species which has been shown to possess episodic-like memory abilities. In our study, 4 cuttlefish were trained in an episodic-like memory task. Each cuttlefish was paired with a control cuttlefish that did not receive training, while being exposed to the same motor and visual stimulations every day. One hour after reaching the learning criterion of the task, the brains of the trained cuttlefish and of its paired control were processed. After a validation of custom-made antibodies, we studied the neuronal activation of the vertical complex, a part of the brain known to be involved in learning and memory, using a new designed neurobiological procedure: comparison of ubiquitin-c terminal hydrolase (a protein known to be a neuronal activation marker in Aplysia) immunoreactivity between trained and control cuttlefish. First analyses showed a higher activation of different lobes of the vertical complex in trained cuttlefish in comparison with their paired control. Our study 1) provides a new method to explore the neuronal substrates of learning and memory in cuttlefish; 2) is the first to explore brain activation following an episodic-like memory task in invertebrates.

Billard, P., Schnell, A., Clayton, N. S., Darmaillacq, A. S., Jozet-Alves, C. (in preparation) Neuronal substrates of episodic-like memory in cuttlefish.

Introduction

Scientific literature provides a significant documentation on mental time travel abilities in animals at the behavioural level. A large range of species have the ability to remember the past (e.g., rats, Fortin et al., 2002; Babb and Crystal, 2006; birds, Clayton and Dickinson 1998; Zinkivskay et al., 2009; primates, Martin-Ordas et al., 2010; pigs, Kouwenberg et al., 2009; dogs, Fugazza et al., 2020; cuttlefish, Jozet-Alves et al., 2013; bees, Pahl et al., 2007, for review see Billard et al., 2019). Whereas 20 years ago some researchers were firmly opposed to the view that animals would possess the capacity to retrieve personal past information (i.e., episodic memory; Suddendorf and Corballis, 1997, Roberts, 2002), their opinions recently evolved with the growing number of behavioural evidence that animals might be able to do so (e.g., Roberts, 2007; Roberts, 2012; Corballis, 2013).

Brain studies have tried to identify the cerebral structures involved in episodic-like memory in vertebrates (e.g., lesions of hippocampus in mice: DeVito and Eichenbaum, 2010; Jin et al., 2020; and rats: Hayashi et al., 2020). Whereas neural substrates of episodic-like memory have been explored in primates (Gaffan, 2007), studies have mostly focused on rodents, and aimed to develop adequate animal models for neurobiological investigation (e.g., Veyrac et al., 2015; Jiang et al., 2018) notably to understand and overcome memory impairment in physiological and pathological aging (e.g., Robitsek et al., 2008). Studies showed for instance the involvement of the hippocampus (e.g., Li and Chao, 2008; for review see Eichenbaum, 2000; 2004), the enthorinal cortex (e.g., Lipton and Eichenbaum, 2008), the prefrontal cortex (e.g., Eichenbaum, 2017 for review on the medial prefrontal cortex-hippocampus circuit see Chao et al., 2020), and the cingulate cortex (e.g., Jin et al., 2020) in episodic-like memory. Studies have investigated how these different regions are differently involved in the what, the where, and the when components of episodic-like memory (DeVito and Eichenbaum, 2010; Chao et al., 2017), but also explores the similarities or differences between neural networks involved in either familiarity or recollection processes (Sauvage, 2010). Similar functional activity was found in the human hippocampus for episodic memory (e.g., Burgess, 2002; Behrendt, 2013), suggesting that the neural basis of episodic memory is shared in mammals.

No studies have yet documented the episodic-like memory neural activations in invertebrates, although episodic-like memory abilities have been observed behaviourally in the common cuttlefish (Jozet-Alves et al., 2013). The cognitive continuity of episodic cognition in mammals, has been suggested to be linked with the continuity of hippocampal function

Billard, P., Schnell, A., Clayton, N. S., Darmaillacq, A. S., Jozet-Alves, C. (in preparation) Neuronal substrates of episodic-like memory in cuttlefish.

(Corballis, 2013). Similar hippocampus-like structure has been found in birds (Colombo and Broadbent, 2000) which have also been evidenced to possess episodic-like memory (e.g., Clayton and Dickinson, 1998; Zinkivskay et al., 2009). Thus, the existence of a common neuronal network of episodic cognition might not be restricted to mammals. Cuttlefish exhibit sophisticated cognitive abilities (e.g., Jozet-Alves et al., 2013; Billard et al., 2020a) while possessing a markedly different brain than those of vertebrates (Dickel et al., 2013). Investigating the neuronal underpinnings of episodic-like memory in an invertebrate would help understanding how this capacity has emerged in various species and whether it is related to particular properties of the neural networks.

Cuttlefish possess highly developed capacities for learning and memory. For instance, researchers have evidenced that they possess different types of learning abilities: non-associative learning (habituation: e.g., Samson et al., 2014; imprinting, e.g., Darmaillacq et al., 2006; Guibé et al., 2012), associative learning in classical or operant conditioning procedures (e.g., Purdy et al., 1999; Cole and Adamo, 2004; Darmaillacq et al., 2004b; Cartron et al., 2013), spatial learning (reviewed in Jozet-Alves et al., 2013), and more recently social learning (Sampaio et al., 2020). It was also evidenced that cuttlefish possess the capacity to encode and retrieve when and where their preferred food is available (episodic-like memory, Jozet-Alves et al., 2013). More recently, it was showed that cuttlefish could retrieve in which modality an item was previously encountered (did I see it or did I smell it?), an ability known as source-memory, (Billard et al., 2020a).

Cuttlefish possess a centralized nervous system composed of around 100-200 million neurons (Budelmann, 1994) dispatched in several lobes. The oesophagus passes through the brain and divides it into a supra- and a sub-oesophageal masses, situated in-between two large optic lobes. In the dorsal part of the supra-oesophageal mass is located the vertical lobe complex, an area known to be involved in learning and memory (Sanders, 1975; Dickel et al., 2001). The vertical lobe complex is constituted of three different lobes: the vertical, the superior frontal, and the subvertical lobes (Figure 36). The superior frontal and the subvertical lobes are centers of multisensory convergence, which send pre-treated information to the vertical lobe (Nixon and Young, 2003). Because the vertical lobe does not receive direct input from the sensory organs or motor effectors, it has also been shown that it is a silent area, which does not react when directly stimulated (Boycott 1961). Ablation of the vertical lobe has been shown to impair visual learning in cuttlefish *Sepia officinalis* (Sanders and Young, 1940). Another study using more localized and reproducible lesions (i.e., electrolytic lesions) aimed to determine the

effect of damaging either the dorsal or the ventral part of the vertical lobe (Graindorge et al., 2006). The authors showed that ventral lesions impaired acquisition of a spatial learning task while dorsal lesions impaired long-term retention of this spatial learning. Ontogenetic studies have shown that the post-hatching growth of the vertical lobe is correlated to an improvement of learning and long-term retention abilities (Dickel et al., 2001). The superior frontal lobe is also involved in learning and memory processes. Agin and collaborators (2001), showed metabolic changes in the superior frontal lobe after an associative learning task (i.e., prawn-in-the-tuve task), suggesting changes in neuronal activity linked to consolidation processes. The tracts between the three lobes composing the vertical lobe complex might play a crucial role in these cognitive abilities. Indeed, stimulation of the superior frontal-vertical lobe tracts have been shown to induce long-term potentiation in the vertical lobe (Shomrat et al., 2011). Moreover, the vertical-subvertical lobe tracts have also been evidenced to play a key role in memory abilities; their appearance is correlated with the emergence of memory during postembryonic development (Dickel et al., 1997), while their degeneration during aging is correlated with memory impairments (Chichery and Chichery, 1992).

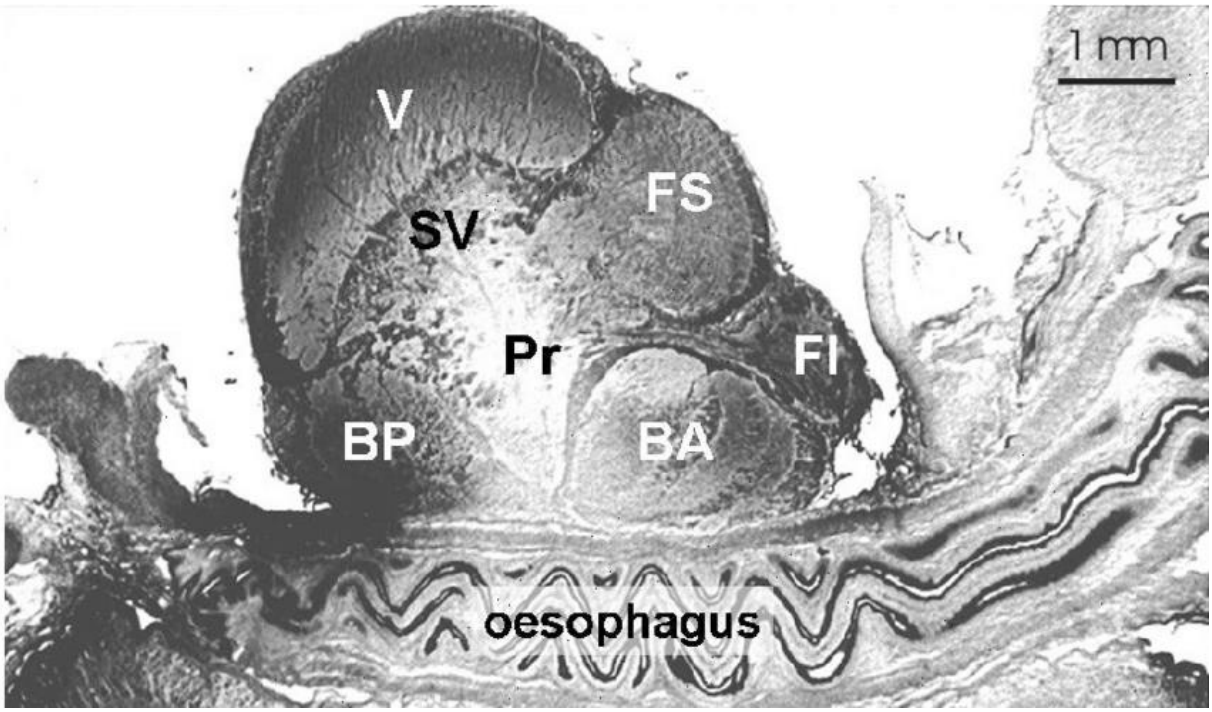


Figure 36 Sagittal section of the brain of an adult cuttlefish, S. officinalis, showing some of the major lobes within the brain. The different lobes of the brain surround the oesophagus. BA & BP: Anterior and posterior basal lobes, FI & FS: Inferior and superior frontal lobes, Pr: Precommissural lobe, SV: Subvertical lobe, V: Vertical lobe. Picture from Agin et al., 2006.

No study has investigated the neuronal underpinnings of episodic-like memory in a species possessing a very different central nervous system than mammals. In our study, we used an immunoreactivity procedure allowing us to map the neuronal activations linked to episodic-like memory while controlling for visuo-motor activations. We focused on the labelling of ubiquitin c-terminal hydrolase in the brain cells of cuttlefish vertical lobe complex as it has been shown to be a marker of neuronal activation in Aplysia (Hedge et al., 1997).

1. Methods

a. Subjects

12 sub-adult European common cuttlefish participated to this study. Cuttlefish were divided in two groups: 6 cuttlefish were part of the trained group and were paired with 6 cuttlefish from the control group. Cuttlefish were reared from eggs in the Marine Biological Laboratory, Marine Resources Centre, Woods Hole, USA (41◦ 31′ N, 70◦ 39′ W). All eggs were collected from the English Channel along the southern coast of England. Dorsal mantle lengths were measured at the beginning of the experiment (mean mantle length ± SEM = 41.79 ± 1.04 mm; range = 29 – 58 mm). Tanks were supplied with a constant flow of filtered seawater (~10 L min-1) and maintained under natural daylight conditions and at a temperature of 15 – 17°C. Prior to the experimental trials, cuttlefish were fed a mixed diet of food items ad libitum including thawed frozen prawn, live grass shrimp, *Palaemonetes paludosus*, live *gammarid shrimp*, *Platorchestia platensis*, and juvenile Asian shore crabs, *Hemigrapsus sanguineus*. Subjects were used in several non-invasive experiments and were housed for the remainder of their life cycle until they died following senescence. Ethical approval was not required for the experiments conducted at the MBL as there are currently no ethical regulations in place for research on cephalopods in the USA. However, experimental procedures planned were submitted and approved ((#22429 2019101417389263 v2) by the French regional ethical committee (CENOMEXA; agreement number 54).

b. Behavioural episodic-like memory procedure

i. Test group

1. Prey preference

We first conducted tests to determine the feeding preferences of each cuttlefish. Dead shrimp and live shrimp were presented simultaneously in the cuttlefish anterior visual field. The left/right positions of the prey were changed randomly. Cuttlefish were presented with this test

Billard, P., Schnell, A., Clayton, N. S., Darmaillacq, A. S., Jozet-Alves, C. (in preparation) Neuronal substrates of episodic-like memory in cuttlefish.

10 times over a period of 3 days (i.e., 3 or 4 times per day). All cuttlefish preferred live over dead shrimp.

2. Pre-training: learning to approach the visual cue to get a food reward

Step 1: To familiarize the cuttlefish with the visual cue (a black and white PVC square, 12 cm x 12 cm) the latter was placed in their home tank during three days.

Step 2: 24 hours later, the visual cue was placed in the tank; after 60 seconds, a prey was placed just in front of it. If the cuttlefish did not catch the prey within 3 min, both the visual cue and the prey were removed from the tank. Step 2 was repeated 4 times a day per cuttlefish. When a cuttlefish went repeatedly close to the visual cue before placing the prey in the tank, cuttlefish went to Step 3.

Step 3: Cuttlefish were then trained to go close (i.e., less than 10 cm) to the visual cue to get food. If the cuttlefish did not approach the visual cue within 4 min, the latter was removed from the tank. Step 3 was repeated 4 times a day per cuttlefish. We considered that cuttlefish had learned the task when they went close to the visual cue in less than 60 seconds after it was placed inside their home tank, at least 8 times over 10 consecutive trials.

3. Training: learning the replenishment rate (replenishment training)

Cuttlefish learned that their preferred prey replenished after a long delay (3 hours) but not after a short delay (1 hour). Two identical visual cues were placed in front of the tank next to each other. One was always associated with dead shrimp, and the other was always associated with live shrimp. During training, each trial was constituted in two consecutive phases, and each cuttlefish received one training trial per day. During the first phase, when the cuttlefish went close to one of the visual cues, a live and a dead shrimp were simultaneously placed in the tank, each one in front of its corresponding visual cue. The cuttlefish was then allowed to capture one of the two preys. The second phase started randomly either after a short (1 hour) or a long delay (3 hours). On trials with a short delay, going close to the visual cue associated with the non-preferred prey was reinforced by giving the cuttlefish the non-preferred prey to eat, but going close to the visual cue associated with the preferred prey was not rewarded (i.e., the prey item was not available for consumption). On trials with a long delay, going close to the visual cue associated with live or dead shrimp, was reinforced by giving the cuttlefish the corresponding prey. A choice was considered correct if the cuttlefish went close to the visual cue associated with dead shrimp after a short delay, and close to the visual cue associated with

shrimps after a long delay. Cuttlefish were trained until they reached an acquisition criterion of at least 8 correct choices in 10 consecutive trials (Binomial test: $p = 0.044$).

4. Episodic-like memory training (ELM training)

The procedure applied was very similar than training (Figure 38a). Each trial was constituted of two consecutive phases, and each cuttlefish received one trial per day. However, this time, the position of the two visual cues varied from trial to trial, in order to make each trial unique. Cuttlefish were trained until reaching the acquisition criterion of at least 8 correct choices out of 10 consecutive trials.

ii. Control group

Cuttlefish from the control group did not receive training concerning the replenishment rate of the shrimp and dead shrimp and ELM training. However, cuttlefish from the control group were exposed to the same visual stimulation (visual cue) and performed the same motor actions than the cuttlefish of the trained group (i.e., catching shrimp and swimming). However, they did not have to memorize the position of the visual cue or learn any delay rule. Each cuttlefish from the control group was paired with one cuttlefish of the trained group and they were both trained and tested simultaneously in two separate tanks. Pairs were euthanized 1 hour after the cuttlefish from the trained group reached the acquisition criterion and their brain was extracted at the same moment. This pairing procedure allowed distinguishing neuronal activation linked to motor/visual stimulation from neuronal activation linked to learning and memory.

c. Brain fixation and sectioning

1 hour after reaching the acquisition criterion (for the trained group), the two paired cuttlefish were anaesthetized by immersion in 2% ethanol in seawater, and killed by decapitation. Each brain was rapidly dissected, and fixed for 16 hours at 4°C by immersion in 4% paraformaldehyde dissolved in 0.2 M phosphate buffer (PB; pH 7.4). They were then rinsed with 0.2 M phosphate buffer, and transferred into a 0.2 M phosphate buffer 20% sucrose solution for 12hr for cryoprotection. Brains were embedded in Tissue-Tek (Miles Scientific, Naperville, IL, USA) and frozen in liquid nitrogen. Frontal sections (15 µm thick) were cut by using a cryostat (CM3050, Leica, Nussloch, Germany), collected on gelatin-coated slides and stored at -80°C.

d. Immunohistochemistry

Sections were rinsed in three consecutive baths of 0.1 M PB during 10 mn. The sections were incubated for 15 min in 0.1 M PB containing 3% BSA and 0.25% Triton X-100. Then, sections were incubated overnight à 4°C, for single-immunohistolabeling with custom-made antibodies raised in rabbit (Proteogenix) against a part of the sequence of Ubiquitin C-terminal hydrolase of cuttlefish (called here sepUCH) diluted at 1/1500 in 0.1 M PB and 0.25% Triton X-100. Sections were subsequently rinsed in three successive baths of 0.1 M PB during 10 min. Incubation with anti-rabbit secondary antibody diluted in 0.1 PB M and 0.25% Triton X-100 at 1:500 was carried out for 2 hours at room temperature. Then, sections were rinsed in three successive baths of 0.1 M PB during 10 min. We then used an avidin-biotin detection kit (Vectastain Elite ABC kit; dilution 1:200 during 30 min at room temperature). Finally, sections went through three consecutive rinses in 0.1 M PB during 10 min, and immersed in 0.05g DAB and 0.2g Nickel with 100 ml TRIS and 50 µl of hydrogen peroxide. Then, sections were mounted in Roth's rosti-histokit, and coverslipped.

e. Images analysis

Images of sections were acquired using a Zeiss axio-imager M2 microscope with ZEN© microscope software. Our regions of interest were situated in the learning centre of the cuttlefish brain (i.e., the vertical lobe complex) comprising the vertical lobe, the superior frontal lobe, and the subvertical lobe.

The images were analysed on ImageJ©. The cortex and the neuropil of the brain region (Figure 37) were detoured and the mean grey level was measured for each region using the mean grey level index, indicating the brightness of a pixel. The lower the grey level, the darker the immunolabeling. Further analyses were made to compare the left and right part pf each studied brain stractures, as it has been shown in literature a lateralized involvement of the hippocampus in episodic cognition. The mean number of analysed sections per cuttlefish was: 54 for the vertical lobe, 80 for the superior frontal lobe and 56 for the subvertical lobe.

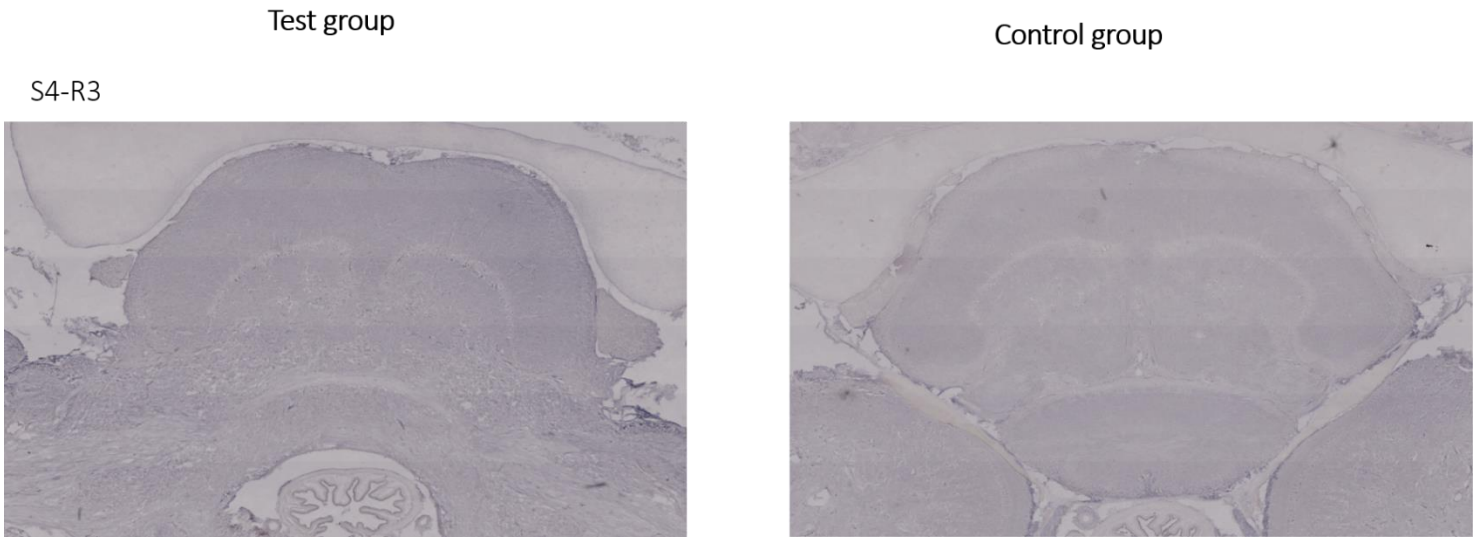


Figure 37 Example of frontal sections of the brain of a trained cuttlefish and its paired control (ubiquitin-c terminal labeling).

f. Statistical analysis

By lack of time, only four pairs of cuttlefish were analysed. This low number of animals does not allow us to conduct any statistical analysis yet. The number of correct choices during the episodic-like memory training was analysed on R software (version 3.5.1) using binomial tests (binom.test function on R).

2. Results:

a. Episodic-like memory test:

Cuttlefish reached the learning criterion in 16 trials in average. Cuttlefish chose significantly more the visual cue associated with the dead shrimp after 1-h delay (binomial test: $p < .01$, confidence interval, 0.58-0.94) and chose the visual cue associated with the live shrimp after 3-h delay (binomial test: $p = .001$; confidence interval: 0.73- 0.95, Figure 38b).

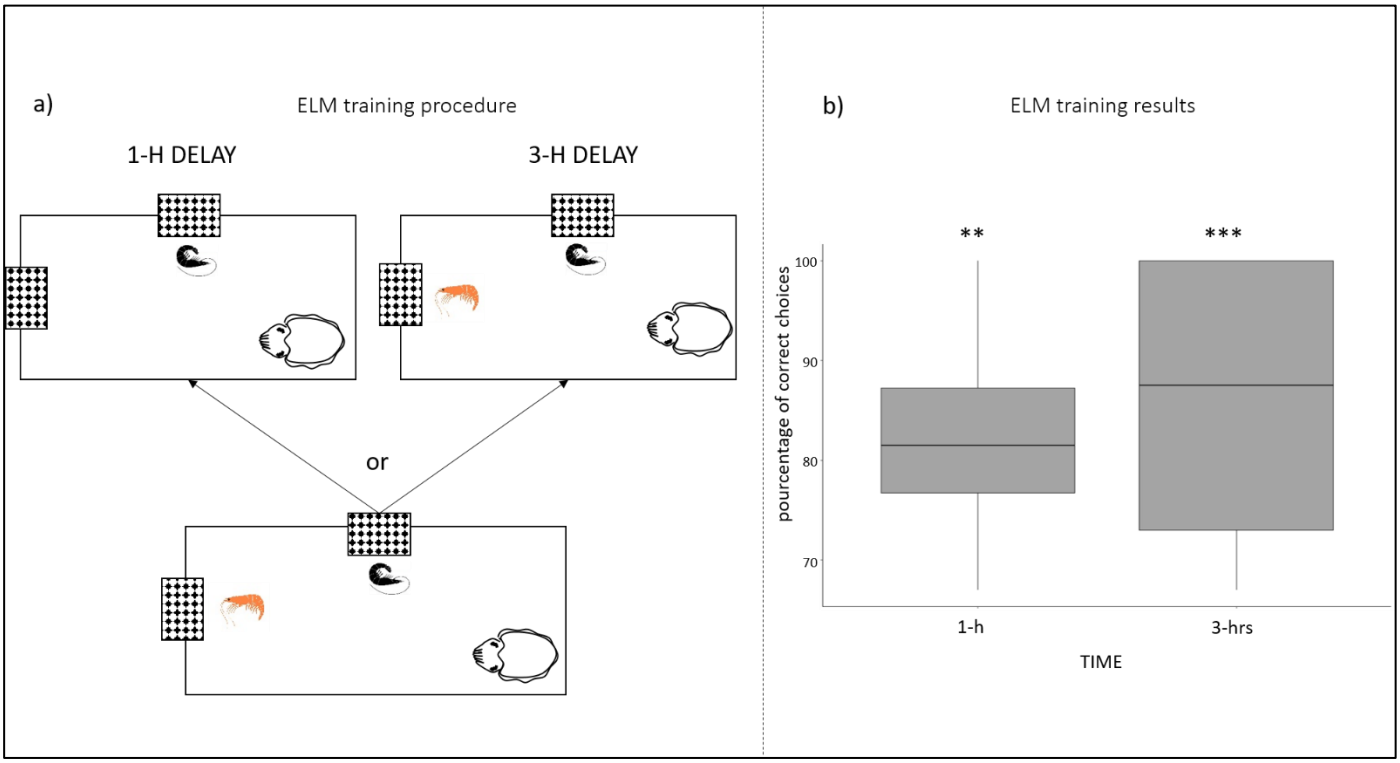


*Figure 38 Design and results of the episodic-like memory experiment. a) Procedure of the episodic-like memory experiment; b) Median percentage of correct choices for the episodic-like memory (ELM) training. Binomial tests: ** <.01; *** =.001*

b. Neuronal activations:

The comparison of the neuronal activation between the left and the right sides of the three lobes of the vertical complex (i.e., the vertical, the subvertical, and the frontal superior lobes) showed no difference either in the trained (Figure 39) or in the control (Figure 40) groups. Thus, we decided to focus on the differences in activation in the three lobes of the vertical complex of the trained and the control groups without differentiating the left/right side for each lobe.

Neuronal activations seemed greater in the trained group than in the control group in the vertical (VL, figure 41), the subvertical (SV, Figure 42), and the frontal superior (SF, figure 43) lobes.

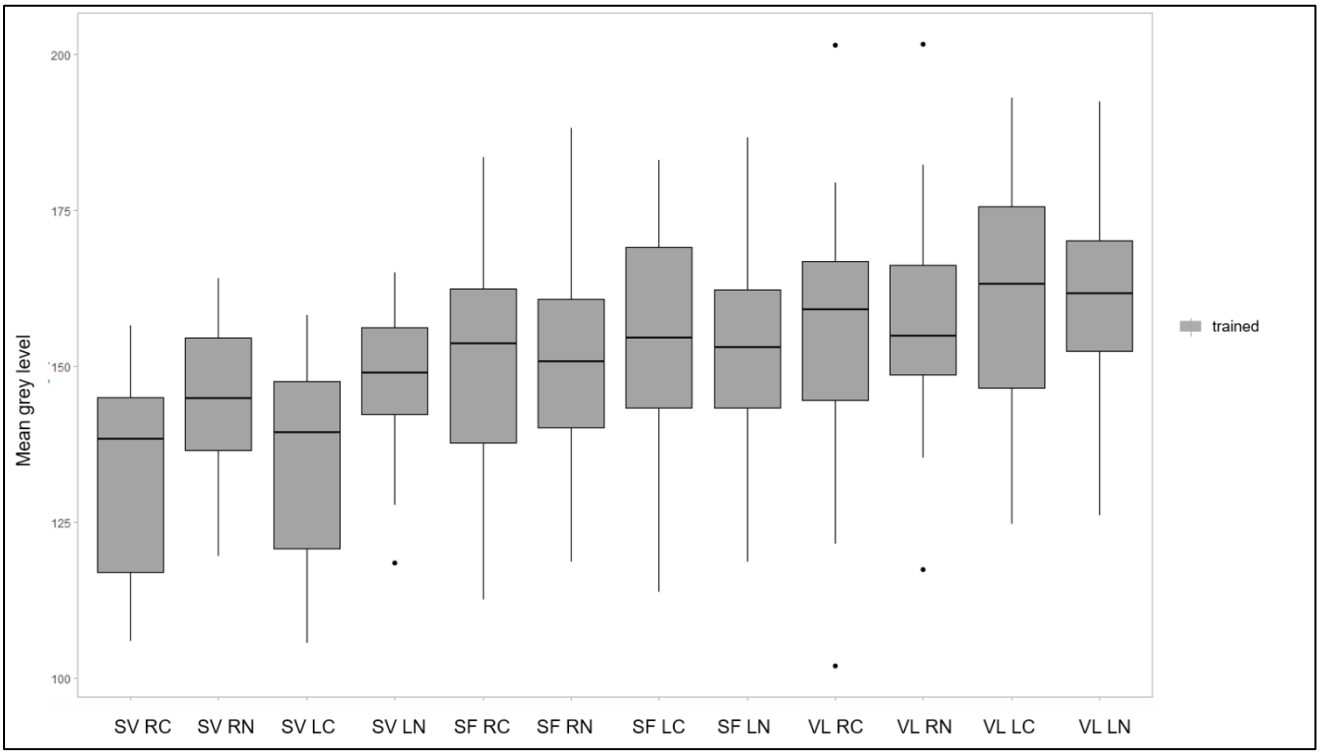


Figure 39 Median grey level of each side of the lobes in the cortex and the neuropil in the trained group. SV RC= Right subvertical lobe cortex; SV RN= Right subvertical lobe neuropil; SV LC= Left subvertical lobe cortex; SV LN= Left subvertical lobe neuropil; SF RC= Right superior frontal lobe cortex; SF RN= Right superior frontal lobe neuropil; SF LC= Left superior frontal lobe cortex; SF LN= Left superior frontal lobe neuropil; VL RC= Right vertical lobe cortex; VL RN= Right vertical lobe neuropil; VL LC= Left vertical lobe cortex; VL LN= Left vertical lobe neuropil.

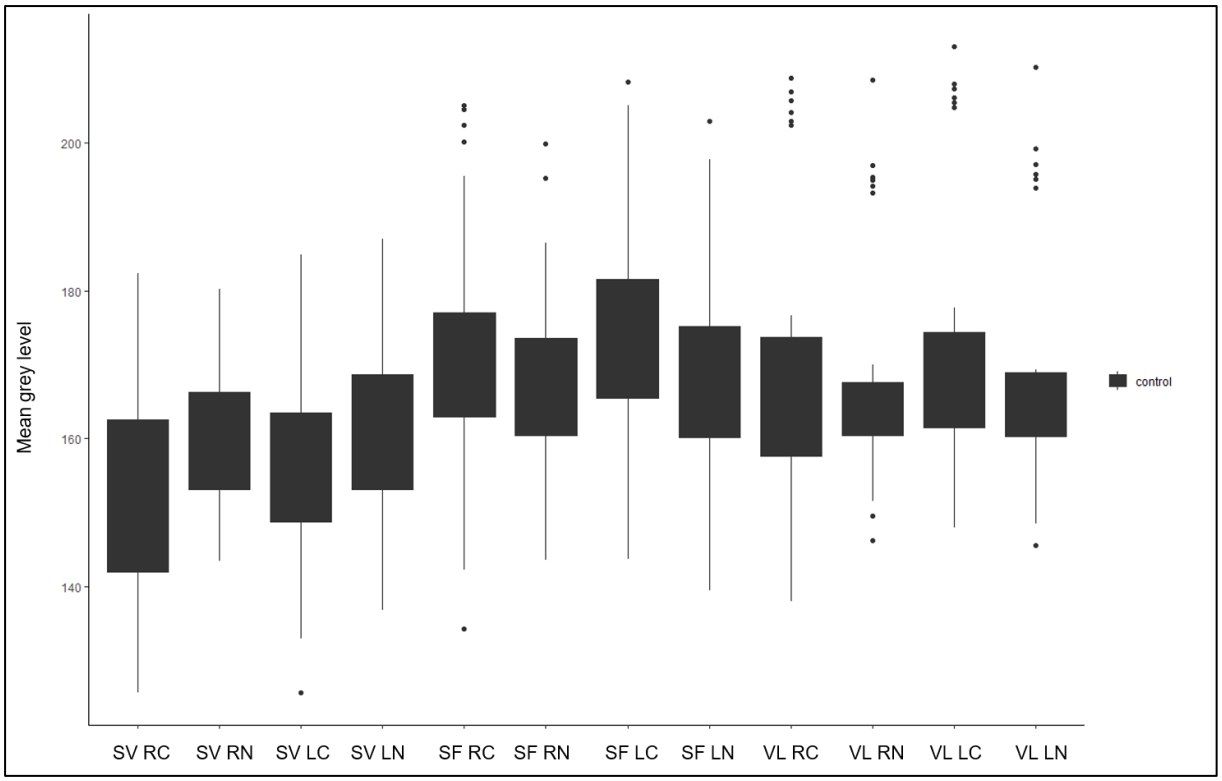


Figure 40 Median grey level of each side of the lobes in the cortex and the neuropil for the control group. SV RC= Right subvertical lobe cortex; SV RN= Right subvertical lobe neuropil; SV LC= Left subvertical lobe cortex; SV LN= Left subvertical lobe neuropil; SF RC= Right superior frontal lobe cortex; SF RN= Right superior frontal lobe neuropil; SF LC= Left superior frontal lobe cortex; SF LN= Left superior frontal lobe neuropil; VL RC= Right vertical lobe cortex; VL RN= Right vertical lobe neuropil; VL LC= Left vertical lobe cortex; VL LN= Left vertical lobe neuropil.

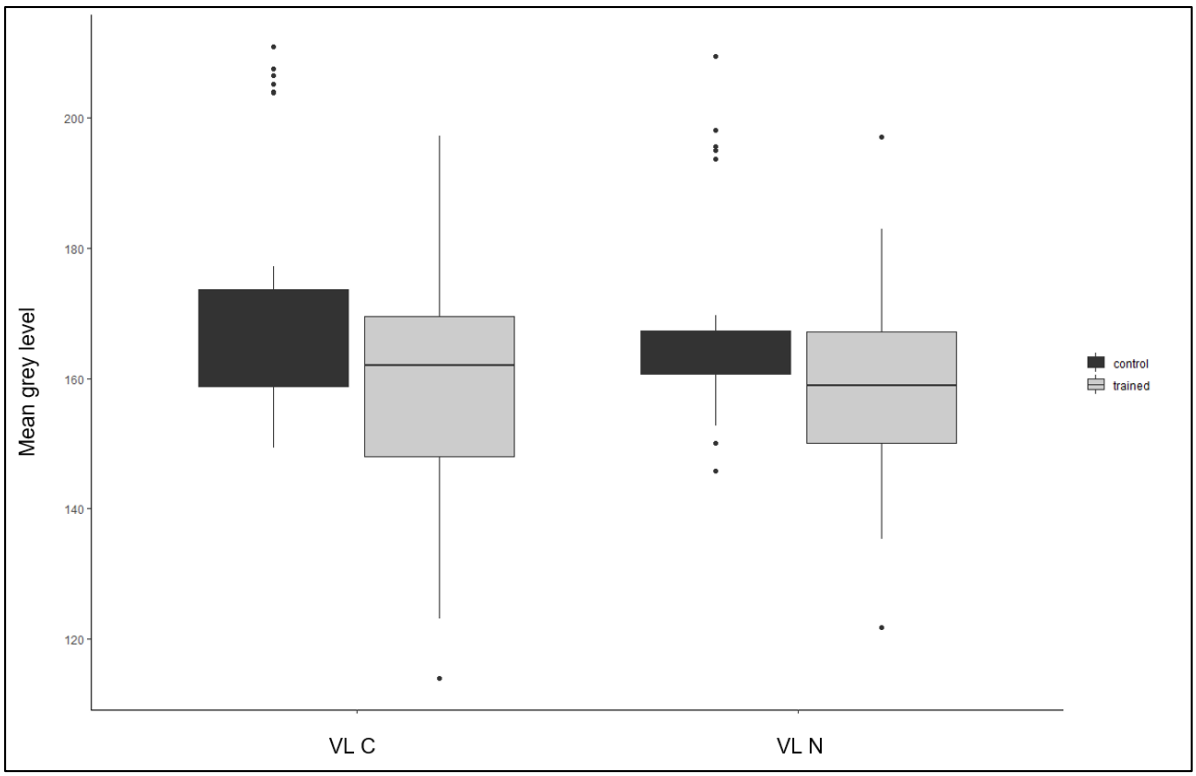


Figure 41 Median grey level in the cortex and the neuropil of the vertical lobe for the trained and the control groups. VL C= Vertical lobe cortex; VL N= Vertical lobe neuropil.

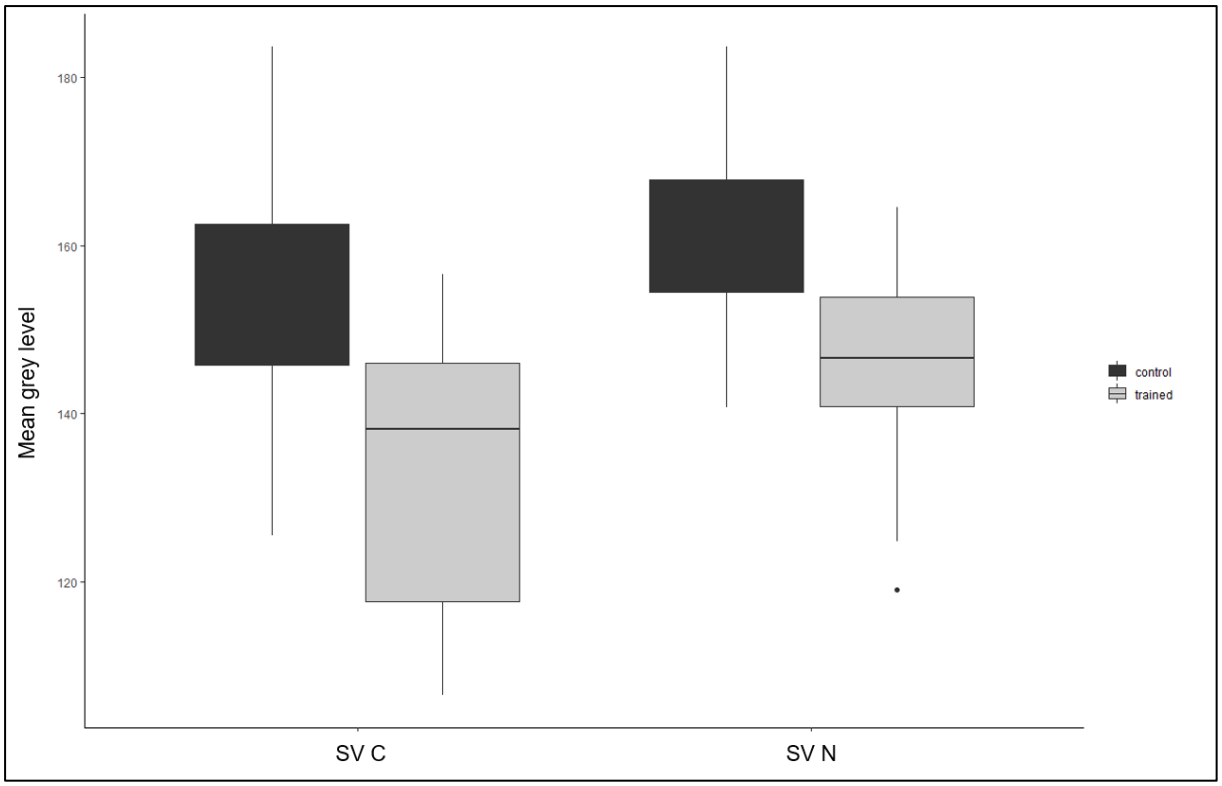


Figure 42 Median grey level in the cortex and the neuropil of the subvertical lobe in the trained and the control groups. SV C= Subvertical lobe cortex; SV N= Subvertical lobe neuropil.

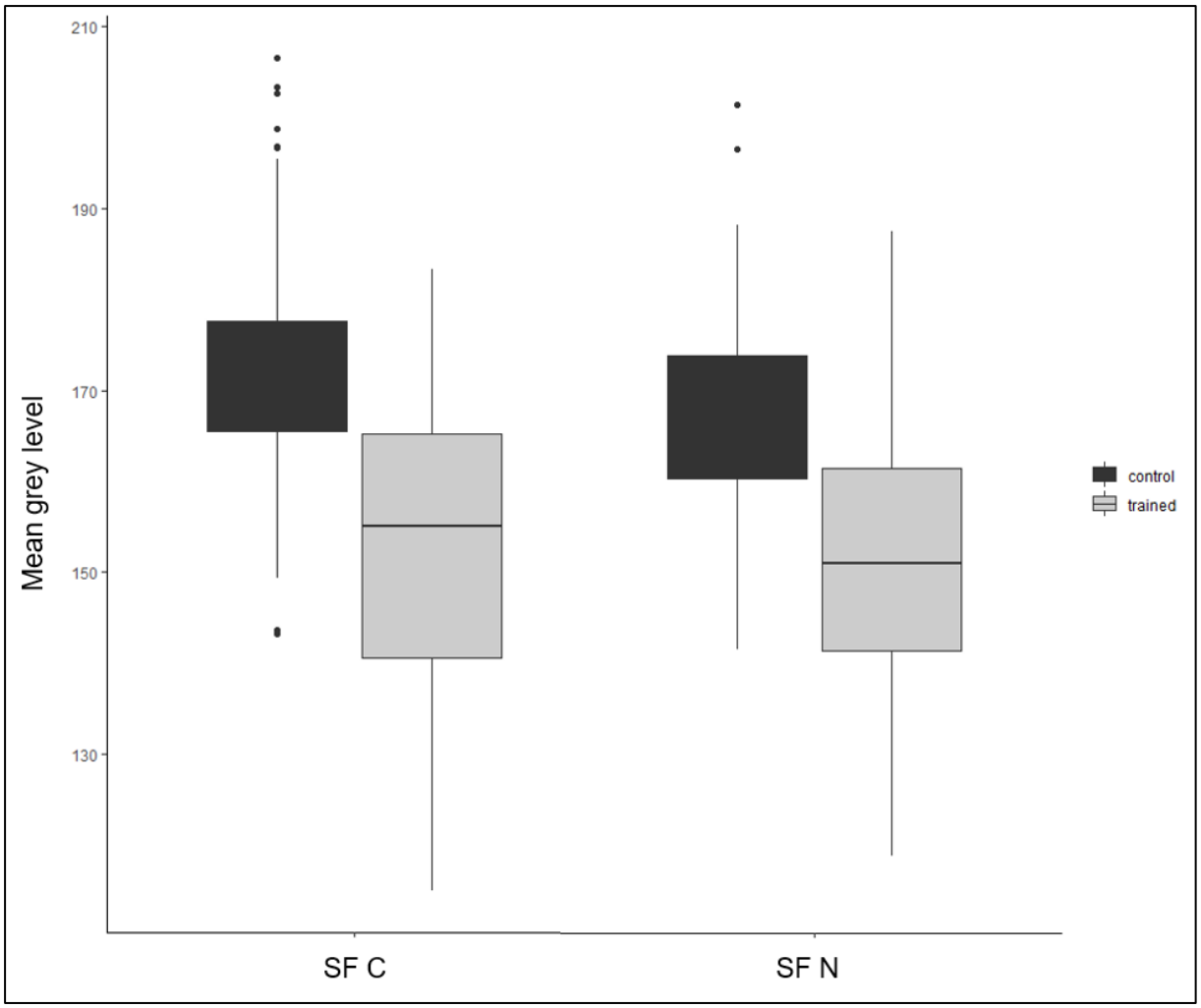


Figure 43 Median grey level in the cortex and the neuropil of the superior frontal lobe in the trained and the control groups. SF C= Superior frontal lobe cortex; SF N= Superior frontal lobe neuropil.

3. Discussion:

At the behavioural level, our results showed that all cuttlefish from the ELM trained group were able to perform the episodic-like memory task. All cuttlefish from the trained group significantly chose the visual cue associated with the non-preferred prey when tested after 1 hour, and significantly chose the visual cue associated with their preferred prey after 3 hours. These results show that cuttlefish were able to remember what type of prey (i.e., live or dead shrimp) they encountered, where, and how long ago (i.e., 1-h or 3-hrs delay). At the neurobiological level, our study presents a higher level of *UCH* immunolabeling in the vertical lobe, the superior frontal lobe, and the subvertical lobe in the trained group (i.e., cuttlefish who passed the episodic-like memory training), in comparison with the control group.

Our experiment replicated the original behavioural study of episodic-like memory in cuttlefish (Jozet-Alves et al., 2013), confirming that cuttlefish can remember what type of prey was encountered, where, and how long ago. The cuttlefish did not solve the task using circadian rhythm (Babb and Crystal, 2006) as they were not always tested at the same time of the day, and could not use the smell of the prey to choose the visual cue (as the prey were placed in the water only when the cuttlefish already made its choice). Moreover, this test cannot be explained by relative satiety because cuttlefish still chose the less-preferred prey after the 1-h delay.

Our study describes for the first time that the expression of ubiquitin c-terminal hydrolase can be used as a marker of neuronal activation in cephalopods. In Aplysia, it has been shown that *Ap-Uch* is an immediate early gene crucial for long-term facilitation (Hedge et al., 1997). In mice, Uchl3, an ortholog of *Ap-Uch*, plays a role in spatial learning and working memory in rodents (Wood et al., 2005). In our study, the fact that the three lobes of the vertical complex show a higher level of immunohistolabeling in trained versus control group suggests that *sepUch* is an inducible gene, and that it might be a functional analog of *Ap-Uch*. This higher level of labelling in the three lobes of the vertical complex in the trained group suggests an involvement of these lobes in learning and memory processes. Indeed, cuttlefish from the control group were exposed to the same visual (visual cue, sight of prey), and motor stimulation (swimming behaviour, motor sequence involved in prey catching with the tentacles). Only four pairs of cuttlefish have been studied by now, and these analyses should be followed to confirm this. Furthermore, to show a specific involvement of these lobes in ELM training, it will be necessary to analyse the grey level in other parts of the brain. This will make us able to determine whether there is a generalized activation of the central nervous system when doing the ELM task, or whether it is specifically the case for these three lobes of the vertical complex.

Our study seems to confirm the vertical lobe's implication in learning and memory processes as it has been shown in several studies available in the scientific literature. First, ablation or lesions of this lobe impaired the acquisition of an associative task and of spatial learning task as well as long-term retention of a previously learned task (Sander and Young, 1940; Graindorge et al., 2006). However, these methodologies used were highly invasive and have damaged surrounding cells and fibres which makes difficult to state on the role played by the vertical lobe in these studies. The maturity of the vertical lobe has been correlated with low performances in long-term memory (Dickel et al., 2001). It was also evidenced that the vertical lobe is the center of long-term potentiation (Shomrat et al., 2011). Our study confirms the implication of the vertical lobe in the acquisition and the retention of long-term memory.

Billard, P., Schnell, A., Clayton, N. S., Darmaillacq, A. S., Jozet-Alves, C. (in preparation) Neuronal substrates of episodic-like memory in cuttlefish.

Moreover, our study provides a non-invasive methodology, using a replicable and controlled procedure, allowing us to evidence cuttlefish neural activations without damaging the brain. Further studies should investigate the role played by ventral and dorsal parts of the vertical lobe as it has been shown that they present different functions in memory processes (i.e., the ventral part would be linked with acquisition of learning while the dorsal part would be linked with long-term retention of this learning, Graindorge et al., 2006).

Lesion studies have investigated the role of the frontal superior lobe in learning abilities in octopus (Grey and Young, 1964; Maldonado, 1965; Nixon and Young, 1966). However, only one study has evidenced its involvement in learning and memory processes in cuttlefish (Agin et al., 2001). This study showed enhanced cytochrome oxydase labelling activity in the superior frontal lobe after the prawn-in-the-tube learning task in cuttlefish. The cytochrome oxydase is a mitochondrial enzyme involved in phosphorylation processes which has been described as a marker of long-term neuronal activity. In cuttlefish, the frontal superior lobe receives sensory inputs from the arms (Budelmann and Young, 1987). Dickel and collaborators (2001) discussed the possible role played by the integration of nociceptive inputs coming from arm-related movements (e.g., catching the preys) with the enhancement of learning. Indeed, they argued that the superior frontal lobe may act as an "amplifier" of nociceptive inputs when the cuttlefish is striking its tentacles to catch a prey. In our study, cuttlefish could catch preys in both trained and control groups. Thus, the different levels of activation of this lobe in the trained and the control groups would be less likely explained by its relation with the strikes of the tentacles to catch preys during the experiment. Our result tends to show that the frontal superior lobe plays a role in memory independently of the motor actions performed by the cuttlefish.

Our study showed higher level of activation of the subvertical lobe in the trained than in the control group. The subvertical lobe is connected to the vertical lobe through tracts of fibers. The development of these tracts has been demonstrated to be correlated with the emergence of memory ability (Dickel et al., 1997). When these tracts present numerous degenerative fibers in senescent cuttlefish, an impairment of long-term memory has been observed (Chichery and Chichery, 1992). However, no studies have already shown the implication of the subvertical lobe itself in learning and memory processes. This lobe sends pre-treated information to the vertical lobe. Our study is the first to evidence the implication of the subvertical lobe itself in a long-term memory task. Further studies should investigate its activation in various multisensory memory tasks to better understand its implication in long-term memory processes.

In humans, episodic-memory acquisition and retention has been linked to a neuronal network involving the hippocampus (Kinsbourne and Wood, 1975; Squire and Zola-Morgan, 1991; Eichenbaum, 2001). Hippocampus has been reported to be involved in various tasks such as spatial and episodic-like memory tasks (e.g., Burgess et al., 2002). The vertical lobe system has been shown to be involved in spatial learning, and in the present experiment in episodic-like memory. This complex constituted of three interconnected lobes has often been compared to the mammalian hippocampus, considering some morphological convergence (Young, 1991). Electrophysiological studies undertaken in coleoids have also suggested an evolutionary convergence of the networks involved in activity-dependent long-term plasticity (Shomrat, 2015). Our study goes further in these parallel findings by suggesting its central role in complex cognition, with an implication in ELM in cuttlefish. This vertical lobe complex appears as a good candidate to assess how networks have evolved to reach complex common cognitive abilities. Further studies are now needed to compare cellular and molecular processes involved to determine whether the vertical lobe complex of the cuttlefish presents similar mechanisms that the human neuronal network in episodic cognition. Understanding this differences and similarities in the functioning of these networks in mammals and cephalopods will be helpful to determine the neural prerequisites of complex cognition, and how such networks have been shaped by evolution.

To conclude, our study provides a new procedure allowing us to investigate the neural activations in cuttlefish brain in a reproducible, controlled, and non-invasive manner. Even though we need to complete this study with more individuals and add measures of other lobes, this method is a great tool to explore the neural underpinnings of learning and memory in a cephalopod.

GENERAL DISCUSSION

This PhD thesis aimed at providing new data on mental time travel in common cuttlefish (*Sepia officinalis*) and Eurasian jays (*Garrulus glandarius*). First, it aimed at increasing our knowledge about episodic-like cognition in cuttlefish because there was a real lack of data in the scientific literature. Except for one exception study (cuttlefish, Jozet-Alves et al., 2013), no studies investigated episodic-like cognition in invertebrates. As flexibility is one crucial criterion for episodic-like cognition in animals, we have investigated cuttlefish ability to flexibly adapt their predatory behaviour under different experimental conditions. As episodic-memory is tightly linked with prospective behaviour (e.g., Race et al., 2011) we also studied cuttlefish capacity to act in the present using past experience to plan the future.

A lot of studies have investigated jay's episodic-like cognitive abilities. However, incidental encoding was never investigated in this species even though it is a crucial defining feature of episodic memory (Zhou et al., 2012). As jay is a renowned model of episodic-like cognition, comparing their performance to those of cuttlefish provides a broader view on how this ability might have evolved in different species.

A substantial part of my thesis focused on source-memory. This capacity has not been studied in animals except in two groups of mammals: rodents and primates. Yet, source-memory allows us to investigate the episodic-like cognition with a different point of view because it requires animals to focus on their own perceptions while retrieving a previously encoded event. In this discussion, I will first come back on the different studies on source-memory that have been performed in this PhD thesis, and briefly discuss the definition of source-memory in animals. Then, I will focus on mental time travel in animals and come back on the different behavioural criterions of episodic-like cognition. I will then discuss how we investigated different aspects of mental time travel in cuttlefish, namely flexibility and future-planning. I will conclude with a discussion on the comparison of mental time travel in the common cuttlefish and the Eurasian jay.

I. Source-memory in animals

Chapter 1 presents two ways of exploring source-memory. Firstly, cuttlefish were asked to retrieve whether they smelt or saw a previously encountered item. Results showed that cuttlefish were able to retrieve the modality of presentation in which an item was presented 3 hours earlier. Secondly, we used an incidental learning procedure to investigate whether jays were able to incidentally encode and retrieve a contextual cue, even if it was previously irrelevant to solve the task. Our results showed that males were able to do so, while female were not. In this part

of the discussion, we will come back in more details on these experiments, and discuss the relevance of these protocols to investigate source-memory in animals.

a. Cuttlefish

The first study presented in Chapter 1 reveals that cuttlefish are able to discriminate between two modalities (i.e., vision and olfaction), and memorize in which modality an item was previously encountered (i.e., seen or smelt).

Methodological relevance and limitations

Our protocol introduces a new original way to investigate cuttlefish capacity to retrieve the perceptive source of a previously encountered item (i.e., did I see it or did I smell it? Source-memory for perceptive signals, Johnson et al., 1993). During training, cuttlefish were presented with different items and had the opportunity to report whether these items were presented in the visual or the olfactory modality to receive a reward. At test, cuttlefish were presented with new items, without the possibility to indicate in which modality they were presented. After a delay, they had the opportunity to retrieve from which source (i.e., visual or olfactory modality) the items were previously encountered.

This procedure reminds the item *vs* source tasks in humans (e.g., Jurica and Shimamura, 1999; Macklin and MacDaniel, 2005). In these tasks, individuals first study a list of items (presentation phase, e.g., words) which present different characteristics (e.g., words in different colours). After a delay, participants are presented with new (distractors) and old (target) items and they are asked to indicate whether these items were previously encountered during the presentation phase. In a subsequent source-memory test, participants are asked to retrieve the source of the already encountered items (e.g., in which colour was the word presented?). In both cuttlefish and human tasks, subjects are presented with the items during a presentation phase, and are asked to retrieve the source of the items after a delay in a test phase (i.e., "what was the colour of the word?" for the human task; "what was the modality of presentation of the item?" for the cuttlefish task). One limitation of both human and cuttlefish experiments is that they involve the retrieval of only one source-aspect of the items (e.g., colour and modality). In real life, source-memory allows us to retrieve several aspects of the previous event such as the context in which it happened (where and when), perceptual features (visual, olfactory, auditory information), emotional features and so on. Thus, the next step for studies focusing on source-memory in humans and other animal species would be to investigate whether an individual can

retrieve simultaneously several features from an event: the perceptual and the contextual features for instance (did I see it or did I smell it and in which context?).

One difference between our study and the item *vs* source tasks used in humans can be found during the study phase where subjects are pre-exposed to the source characteristics. In our study, cuttlefish were explicitly asked to focus on the source during training and extensively trained to report which source was associated with the item (i.e., visual or olfactory presentation?). In the human tasks, participants are usually not directly asked to associate the items with the sources during the study phase. In the majority of studies, a list of items is presented to the participants (e.g., list of words, objects, images) who are asked to make a judgement on it (e.g., are the sentences emotional? Davidson et al., 2006; do the words refer to an animal? Guo et al., 2006). However, this judgement is not related to the source of the items (e.g., the gender of the voice who said the sentence, Davidson et al., 2006; the background displayed behind the word, Guo et al., 2006) but is used instead by the experimenter to make the participants focus on a particular feature of the item without focusing on the source. In some exceptions, participants are explicitly asked to associate the source with the items. For instance, in one study, participants were instructed to remember that the visual shapes appeared on the left or right part of the screen, which was the source to retrieve during the source-memory task (Davachi et al., 2003).

Another difference between our cuttlefish study and the item *vs* source task in humans is the nature of the source retrieved. In the item *vs* source task, human participants only focus on *external* information (colour of words, location on a screen, gender of voice). Sometimes, the effect of internal sensation is involved in the study phase but is not the source to remember *per se*. For instance, Doerksen and Shimamura (2001), have investigated the effect of emotional words in participant's capacity to retrieve the source of the word (i.e., colour of words). On the contrary, our protocol focuses on cuttlefish capacity to retrieve *internal* perceptions (did I smell it or did I see it?). This important aspect of our design provides the first evidence that an animal is able to discriminate between two sensory modalities (for further discussion on this topic, see the discussion part of the article in Chapter 2). Furthermore, this focus on internal perceptions has not been emphasized in the study of episodic-like cognition. Indeed, in the episodic-like memory tasks, animals need to retrieve external features such as where and when a type of food was encountered (Clayton and Dickinson, 1998). However, perceptions are inherently linked to episodic memories and the retrieval of our own perceptions might be tightly linked to the feeling

of self. I will discuss this further in the section 3 “How to define source-memory in animals?” of the discussion.

Our experimental procedure presents an innovative way to investigate episodic cognition. According to the literature, episodic memories are created after the attendance of a single event (Crystal, 2010). Thus, episodic-like memory tasks must provide evidence that the animal’s memory is from a specific earlier event. More specifically, it is important to rule out explanations in terms of learning that do not require episodic memory. To do so, authors argued that the episodic-like memory task must include tests based on the retrieval of features encoded during a single event presentation and/or use an unexpected question (Zentall et al., 2001; Singer and Zentall, 2007; Zentall et al., 2008; Zhou and Crystal, 2011). In our study, cuttlefish were tested using new items they never encountered before. Thus, cuttlefish performance in the source-discrimination test was the result of its memory from a single presentation. Furthermore, the source-discrimination test was completely unexpected. Indeed, cuttlefish were trained repeatedly with the same procedure: they were presented with an item and could concomitantly report whether it was presented in the visual or in the olfactory modality. At test, the procedure changed: they were presented with a new item, and did not have the possibility to report under which modality it was presented. It was only after a delay that they could report whether they previously saw or smelt the item. The unexpected nature of the test obliged the animal to retrieve the information using episodic memory and could not apply a simple rule to determine whether the item was previously seen or smelt (Crystal 2018).

To conclude with the methodological aspects of the source-memory experiment in cuttlefish, we can mention one major limitation. The final source-memory test is performed through cuttlefish choice between two visual cues placed in the tank. While all tested individuals (n=5) succeeded to choose the correct visual cue in our study, they had 50% chance to choose the correct visual cue event. Using a third perceptive modality would be a way to circumvent this, however it appears extremely complicated from a methodological standpoint to expose cuttlefish to vibrations of a prey without relying on visual or olfactory cues. This bias can be countered when the number of tested individuals is important. In our study, the number of tested individuals was not high, partly because the study lasted for one year and it would have been difficult to replicate the experiment the following year in the timespan of the PhD thesis. It seems crucial for this study to be replicated with more individuals to confirm or infirm the results found, and to associate a second event feature to the task.

b. Jays

In the second study included in Chapter 1, we focused on an incidental encoding procedure to investigate whether jays could retrieve in which context they saw a specific type of image (i.e., source for contextual information). Results showed unexpected differences between males and females with males being slower to learn the associative learning task (i.e., bird *vs* tree images), but managed to pass the incidental encoding test (i.e., which picture did you see in this context?). Females, although faster to learn the discrimination rule, seemed to answer at random when asked to retrieve which picture was seen in a specific context.

Methodological relevance and limitations

Incidental encoding is a crucial defining feature of episodic memory. Indeed, episodic memories are not usually deliberately encoded (Zhou et al., 2012). For instance, when recalling what you did last week-end, you can remember a lot of different features even if you did not focus on it when this event memory was encoded. In our previous source-memory study, cuttlefish were trained to associate the perceptive modality of the event with a visual cue. While during the source-memory test they did not have the opportunity to select the appropriate visual cue concomitantly with the item presentation, the correct retrieval of the sensory modality after a delay might have been facilitated, because cuttlefish were trained to focus on the sensory modality to receive a reward during training. To complete our previous findings, we aimed to design a study to investigate whether jays could incidentally remember a contextual source.

First, our study provides a new way to investigate incidental encoding in jays. Our procedure included an associative learning phase. During this phase, jays had the opportunity to associate two types of pictures with a yellow or a blue perch. The pictures differed not only in the type of the object they showed (bird, or tree), but also in the colour (coloured or black-and-white picture), and orientation (landscape or portrait). It makes impossible to state whether jays can discriminate between bird and tree semantic categories, however, it was done this way to make the discriminative task easier to learn for the jays. Indeed, the picture discrimination could be based on several features. The source (i.e., a geometric contextual cue placed on the wall) was not relevant during training and jays were thus not trained to focus on it. The contextual cue only became relevant during the unexpected incidental encoding test where jays had to use their episodic memory of the contextual cue to retrieve the type of picture encountered when the cue was present. This procedure differs from other incidental procedures presented in literature (e.g., Zentall et al., 2008; Fujita et al., 2012; Takagi et al., 2017; Sluka et

al., 2018) where the to-be-incidentally-encoded material is pre-exposed prior to test. For instance, in one study, dogs were presented with human simple action and were trained to reproduce the action when it was commanded ("do as I do", Fugazza et al., 2016). In-between the training and the test, they were trained to perform another action (sit down) after witnessing the action of the owner. At test, they were unexpectedly asked to imitate the action of the owner with the command "do as I do". It is possible that dogs incidentally encoded the characteristics of the human action even though it was irrelevant as dogs were asked to sit after witnessing the event. However, as dogs were previously trained to reproduce the human action prior to the test, it is also possible that dogs focused on it when it was performed. The design of our study ensures that birds will need to look back in their episodic memories to retrieve the information required (Crystal 2018; Singer and Zentall 2007; Zhou et al., 2012).

Our study presents several limitations. As the birds cannot be kept too long in the testing room for their well-being, it was impossible to add a delay at test as we did for the cuttlefish source-discrimination task. This has been made possible in our previous experiment as cuttlefish were tested in their home tank. Finally, because we did not expect any differences between sexes and that it was not the focus of our study, the number of individuals of each sex was low (6 males and 5 females) and it would be worth replicating this study to specifically investigate the role of the sex in discrimination learning and incidental encoding.

Sex differences: are females less good at source-memory than males?

The main result of the study came totally unexpected (i.e., sex differences in the acquisition of the discrimination task and the incidental test). This result showed that females were marginally faster to reach the learning criterion than males, but answered randomly to the final incidental test. On the contrary, males were slower to learn the discrimination rule but they all passed the final incidental test.

Certain types of memory have been shown to be sex-dependent. This is the case of spatial memory (also called episodic spatial memory, Uttl and Graf, 1993) for instance, showing a male advantage (Jones et al., 2003). This male advantage has been observed in a large variety of species (monkeys, Lacreuse et al., 2005; rodents, Conner et al., 2020; Barkley and Jacobs, 2007; Jacobs and Schenk, 2003; birds, Dunlap et al., 2006; Hodgson et al., 2008, and cuttlefish Jozet-Alves et al., 2008), including humans (e.g., Léon et al., 2016). These sex differences can be explained by different factors. Memory is a complex ability that can be affected by stress, attention level, or cognitive strategies for example, and is impacted by physiological and

neurobiological factors (Postma et al., 2004; Jones et al., 2003). No studies yet investigated whether birds' attentional strategies vary in different contexts and differ between males and females. However, literature showed that female rats are more attentive to the variations of the stimuli displayed during a behavioural task (e.g., variation of length of inter-trial interval, display of distracting noise, Bayless et al., 2012). In our study, females might have allocated more attention to the discrimination task, and less attention to the surrounding background, while males might have spent more attentional resources to the background, allowing them to encode the contextual cue presented during the discrimination task.

These differences in strategies have been linked to variations in the hormonal level (Jones et al., 2003). According to the fertility and parental care hypothesis, female reproductive success is enhanced by reduced mobility to conserve energy, and to decrease accident and predation risks (Sherry and Hampson, 1997). Males are more active due to an increase of testosterone, which enhance their territoriality and aggressive behaviour towards other males (e.g., Meddle et al., 2002). The jays in our study were about to breed. They started to pair up and share their food, which is a typical behaviour observed in Eurasian jays during the breeding season. Thus, it is possible that our birds used different strategies to solve the task depending on their hormonal level. Studies showed that the hippocampal volume is correlated with the sex having the higher spatial demands (rodents: Jacobs et al., 1990; cowbird, Reboreda et al., 1996; magpie and jackdaw, Healy and Krebs, 1992; marsh tits, Clayton and Krebs, 1994b; for review see Healy et al., 2005). The size of the hippocampus can also vary with the hormone level expressed by the individual (Koss and Frick, 2017). Testosterone improve the size of the hippocampus, notably the dentate gyrus, and the volumes of cell layers in CA1 and CA3 (Isgor and Sengelaub, 2003). Hormonal level is also correlated with performances in spatial memory and reference memory tasks. For instance, mated female pinyon jays are less accurate than males to retrieve food caches after long intervals (Dunlap et al., 2006, for reviews on sex differences in spatial ability see Jones et al., 2003). The increase in hormones specific to the breeding season (i.e., testosterone and oestrogen) could explain the sex differences we observed in this study. This would imply that outside of breeding season females might be equally able than males to incidentally encode a contextual cue. Further studies will be necessary: 1) to confirm sex-difference in discriminative learning rate; 2) to confirm this sex-difference in attentional processes; 3) to state whether these differences are linked to fluctuating levels of hormones during the breeding season.

c. How to define source-memory in animals?

In humans, source-memory is defined as the capacity to retrieve the source of an event (Johnson et al., 1993; Mitchell and Johnson, 2009). This definition is quite broad and the problem is that it can be interpreted in different ways. For instance, retrieving the source can be considered as retrieving *who* said that information. The individual will need to choose among different possible scenarios which one is the most likely to answer the question (it must be George because George knows a lot about this information as he is working in this field). But retrieving the source is sometimes considered as *how* was the information learnt (did I read it somewhere, was I told this, etc). Here, the source becomes the acquisition of the information. Finally, it can also be retrieving a *specific feature* of an information (e.g., colour of the words, orientation on a screen, etc). In human's item *vs* source experiments, the source represents a characteristic of the previously encountered item (e.g., colour, tone of voice, location on a screen, etc.). This characteristic is often defined as the context of the episode. For instance, Stevenson and colleagues (2020), describe source-memory as "the ability to remember contextual features of an event". Senkfor and Cyma Van Petten (1998) define source-memory as "memory for the context of a learning episode, encompassing perceptual features […], spatial location, temporal sequence of events, and whether an event was imagined or actually took place". Source-memory was also designed as "the contextual details surrounding an item" (Canada et al., 2020), or "memory for the source or the origin of material stored in memory: where, in the larger episodic context" (Zhou et al., 2020).

In animals, it is especially crucial to state on a definition that allows researchers to experimentally investigate it without relying on language. Indeed, without language it becomes very difficult to determine whether the animal's behaviour observed truly reflect the cognitive ability that was meant to be measured. To counter this ambiguity, researchers agree on an operant definition of the ability they aim to assess and on behavioural criteria which need to be tested (e.g., episodic-like memory criteria, Clayton et al., 2003a). In our study of source-memory in cuttlefish, we relied on an operant definition of source-memory. We based our definition on the SMF which gives a modelling of how source-information is retrieved (Johnson et al., 1993; Mitchell and Johnson, 2009). To their view, source-memory can be retrieved by the reactivation of the features composing the original event in mind. This operant definition allowed us to create a non-verbal task in cuttlefish: we hypothesized that cuttlefish would activate source-monitoring processes if they were able to retrieve the perceptive feature of a previous even when unexpectedly asked to do so.

Such as we cannot know whether episodic-like memory in animals is truly like episodic memory in humans because phenomenological aspects of episodic-memory cannot be assessed, we cannot assume that the source-memory abilities revealed in cuttlefish relies on the same mechanisms than source-memory in humans. A crucial point to discuss is the appellation of what we observe and of the task we use in animals. For instance, we did not call the incidental encoding study in birds an investigation of source-memory even though incidental encoding can be a way to investigate source-memory processes. When faced with the same problematic concerning episodic memory, Clayton and collaborators decided to call the capacity to retrieve the what-where-when after a single episode, and to flexibly use the what-where-when representation, the episodic-*like* memory (Clayton and Dickinson, 1998; Clayton et al., 2003b). The "*like"* allows the researcher to talk about the targeted cognitive ability - episodic memory – without pretending that what is observed in the birds refers to similar cognitive ability than in humans. The problem with using the same terminology than the one used in humans is that it implies that the same mechanisms are looked for in animals. Recently, searching for human-like abilities in animals has been criticized and is somewhat obsolete (Shettleworth 2009; Wasserman and Zentall, 2006). The question is not anymore "do the animals possess similar episodic cognition than humans?" but rather "how do the animals apprehend the past, the present and the future, and does it have an ecological explanation?". Thus, when studying source-memory in animals we are in fact not studying source-memory but rather the capacity to retrieve specific features that belonged to a previous episode.

Source-memory is deeply linked to episodic memory. Retrieving an episodic memory always involves source-memory processes because the episodic recall involves reliving mentally the past event and thus retrieving several specific features composing the memory (deliberately or not deliberately). As source-memory is always involved in episodic memory recall, we argue that source-memory could be considered as a fourth criterion to evidence episodic-like memory in animals. This fourth criterion completes the investigation of episodic-like memory in animals because it relies on the content of episodic memories but also get closer to the phenomenology of episodic memory (i.e., elements of consciousness related to episodic memories). Indeed, source-memory is about the retrieval of internal information (e.g., perceptions) which might imply introspective mechanisms (what did I feel?) that recall those involved in self (e.g., Silvia and Guedolla, 2001). When an animal is able to discriminate between his own sensations and remember them later (i.e., like the cuttlefish in our source-memory study), it might be because it is aware of what it feels and can flexibly use its mental

representation later if needed. Thus, source-memory can be a way to get closer to the phenomenological aspect of episodic-memory in animals without relying to language, aspects that were referred to as "empirically intractable" (Martin-Ordas et al., 2020, p.2).

II. MTT in animals

Episodic memory was first described as the capacity to retrieve the spatial-temporal context of a personally experienced event (Tulving, 1972). Building on this definition, Clayton and collaborators (2003a) developed the behavioural criteria for studying episodic-like memory in animals. First, episodic-like memory is defined in terms of the *content* of episodic memories, involving the what, the where, and the when of a previously experienced event (Clayton and Dickinson, 1998). Second, the what, the where, and the when must be bound in an integrated representation (i.e., *structure*, Clayton and Dickinson, 1999c; Clayton et al., 2001b). In other words, when remembering where I was last week-end, I also remember when it was and what I did, and I remember this memory as a whole. Then, this bound representation must be used flexibly in different situations because episodic memory is part of the declarative system which is deliberately accessible and involves a flexible retrieval of information (i.e., *flexibility*, Clayton et al., 2003a).

In this part of the discussion, I will discuss how we investigated the flexibility criterion of episodic-like memory in cuttlefish, and how we assessed the prospective side of mental time travel in cuttlefish. Then, I will discuss the neuronal activations following an episodic-like memory task in this species. Finally, I will conclude this discussion with a comparison of all the aspects of mental time travel that have been investigated in the common cuttlefish and the Eurasian jay.

a. Flexibility

The first experiment of the first study of Chapter 3 (Cuttlefish show flexible and future-dependent foraging cognition) presented an experiment whose aim was to assess cuttlefish ability to flexibly adapt their predatory behaviour according to different conditions. In condition 1, cuttlefish received their preferred prey every night (i.e., shrimp) and their less preferred prey every day (i.e., crab). In condition 2, cuttlefish received their preferred prey randomly at night (i.e., they could not predict when their preferred prey will be available), and their less preferred prey every day.

Results showed that cuttlefish in condition 1 used a selective foraging strategy. They stopped eating the crabs during the day to eat the shrimp at night. In contrast, cuttlefish in condition 2, used an opportunistic foraging strategy maintaining their consumption of crabs during the day and eating the shrimp at night when available. After 16 trials, the conditions were reversed. Cuttlefish that were used to have shrimp every night suddenly received them randomly, whereas cuttlefish that were used to receive shrimp randomly suddenly received it every night. Cuttlefish rapidly adapted their foraging strategy and opportunistic cuttlefish became selective and *vice versa.* This experiment is the first to show that cuttlefish can flexibly and quickly adjust their predatory behaviour to changing environmental conditions. Studies showed that cephalopods can exhibit flexible foraging strategies (for reviews see Amodio et al., 2019; Schnell et al., 2020). For instance, octopus can flexibly change the foraging areas in which they hunt for preys once they have been depleted (Mather, 1991; Forsythe and Hanlon, 1997). They can use different technics to catch preys (Fiorito and Gherardi, 1999; Blustein and Anderson, 2016) and remove prey from their protective shell (Anderson and Mather, 2007). Cuttlefish have been showed to flexibly exhibit different types of camouflage to optimise the number of prey caught (Okamoto et al., 2017). It has also been shown that cuttlefish are capable of number discrimination and that they choose preys according to their quality and level of satiation (Yang and Chiao, 2016). However, our study is the first to show that this flexible behaviour can change so rapidly when environmental conditions are changing.

Cuttlefish life history can be sum up as “grow fast and die young” (or “grow smart and die young” Amodio et al., 2019). They live two years and adapt in various environment. It has been argued that cuttlefish evolved intelligence following predation and foraging pressures (Packard, 1972). The evolutionary history of cuttlefish might have triggered the development of complex cognitive abilities and of flexible behaviours to answer to the challenge of social competition or to complex predatory challenges (Amodio et al., 2019). An illustration from the wild has been given by researchers observing a male cuttlefish that mimicked the pattern of females to escape the attention of the dominant male in order to mate with females (Hanlon et al., 2005). However, it has also been argued that flexible behaviour can be supported by simple cognitive mechanisms (Mikhalevich et al., 2017), and would not reflect complex cognition. For instance, squirrels cache their food when the number of acorns is high or when the competition becomes challenging (i.e., conditioning between some environmental cue and the food storing behaviour). Thus, one needs to be careful and verify that no other explanation can be given to explain the apparently flexible behaviour expressed by animals. In our study, cuttlefish

switched their foraging strategy in less than a week. Whether or not this behaviour reflects complex cognitive capacities, cuttlefish showed that they do not stick to one foraging strategy and can dynamically change it to make it more adapted to their environmental conditions.

b. Future-oriented behaviour and future-planning

Some researchers support the idea that unlike humans, animals cannot imagine the future because they are bound to the present and are not able to act independently of their current motivational state (e.g., The Bishof-Kohler hypothesis, Suddendorf and Corballis, 1997; Suddendorf and Corballis, 2007). For instance, when looking for food or building a shelter, they would do so because of their current motivational state and not future one. These authors state that animals are then unable to imagine the future and to plan ahead.

Tulving (2005) described a test to illustrate the criteria of future planning that makes it unique to humans, that he called the spoon test. The spoon test is based on a story of a child who dreams about a chocolate pudding being served at a party, but she does not have any spoon and is unable to eat it. The next evening, she takes a spoon and put it with her in the bed to be better prepared for the next pudding party in her dreams. The spoon test does not precise whether the girl is taking a spoon under the influence of her current motivation for chocolate or because she anticipates that she will want chocolate later. However, this difference is crucial. If the girl is taking the spoon because she already wants to eat chocolate, it would be driven by her current motivational state and thus not represent future planning. On the contrary, if the girl is taking the spoon because she knows that she will want the pudding in her dreams but she does not want it in the present, it would be the perfect illustration of planning.

Besides this capacity to act independently of one's current motivational state, future-planning must answer three criteria (Clayton et al., 2003a; see also Selter, 2020). Like episodic-like memory, future planning in animals must refer to content, structure, and flexibility. In animals, it is also important to distinguish future planning from natural prospective behaviour (Clayton et al., 2003a) because some future-oriented behaviours might not represent future planning. For instance, migrations or hibernation would not necessarily imply planning capacities because young animals which have never experienced winter can innately display some future-oriented behaviours such as collecting food or migrating to the South.

In Chapter 3, the second experiment of the first article (Cuttlefish show flexible and future-dependent foraging cognition) revealed that cuttlefish were able to flexibly orient their predatory behaviour according to different experimental conditions and could take the decision

to eat or not the crabs during the day according to the future availability of shrimp at night. This behaviour seems to show that cuttlefish were acting in the present in function of future predictable conditions, especially because their decision did not follow their natural satiety: when they chose not to eat the crabs during the day, they did so even if they did not eat the previous night (i.e., no shrimp available). While our study shows that cuttlefish can act independently of their current general level of satiety, it does not allow us to determine whether cuttlefish were acting independently of their current desire for shrimp. In other words, when cuttlefish decide not to eat the crab, it might be because they already want to eat shrimp. Thus, our study does not allow us to completely rule out the Bishof-Kohler hypothesis. However, because cuttlefish are taking a decision according to future experimental changes, we can say without taking too much risks that their behaviour is future-dependent.

To counter the issue of this experiment, we designed another study aiming at investigating future-planning in cuttlefish by controlling the satiety of the animal prior to the test (Exploration of future-planning in the common cuttlefish). In this study, juvenile and adult cuttlefish which have been fed to satiety, were given a choice between two desirable options. The first option was to go in the arm of a Y-maze where the cuttlefish might be able to hide in a shelter (shelter arm). The second option was to go in the other arm of the Y-maze where the cuttlefish might be able to eat shrimp (food arm). Once the choice was made, cuttlefish were locked in the chosen arm during the night. In the food arm, cuttlefish could eat the shrimp later at night, whereas no food was delivered during the night in the arm with the shelter. This choice was repeated a second time.

Results showed that all cuttlefish initially preferred to go into the shelter arm. This shows that cuttlefish are strongly attracted by shelters to avoid open and lit areas when they cannot bury in the sand. Studies demonstrated this very strong attraction for shadow can even be used as a positive reinforcement (Alves et al., 2007; Jozet-Alves et al., 2008; Cartron et al., 2012). This choice for the shelter arm answered to the current need of the cuttlefish because they did not know that they will be locked inside all night without having access to food. When exposed to this choice experiment a second time, the shelter arm was not preferentially chosen by the cuttlefish. This tends to show that cuttlefish choosing the food arm the second day were planning for the future, acting according to their future desire for food at night (i.e., cuttlefish were fed to satiety before being asked to choose one of the two arms). It was then very important for us to test whether our results could be explained by a simple associative mechanism: a shelter arm avoidance behaviour, which might have been associated to a negative reinforcement

(no food) the first night. This hypothesis was ruled out because an additional test showed that cuttlefish were still attracted by the shelter arm. This suggests that they truly decided to choose the food arm the second day. An increasing number of studies seems to reveal that animals are able to anticipate the future. For instance, chimpanzees can make tools and save them for later use (Mulcahy and Call, 2006). In another study, chimpanzees and orangutans showed that they were able to override their immediate needs for future ones (Osvath and Osvath, 2008). However, these future-oriented behaviours have been questioned to really represent planning and some authors argued that it could be explained in terms of lower mechanisms such as associative learning (Suddendorf et al., 2009; Suddendorf and Corballis, 2010). In our study, we controlled for the shelter attractiveness in a third choice between an arm of the Y-maze providing a shelter and an empty arm. Results showed that cuttlefish preferentially chose the arm with the shelter. This indicates that cuttlefish did not associate the shelter arm with a negative reinforcement during the second night where they were locked in this arm without food. This control rules out an explanation in terms of lower mechanism in our study. In cephalopods, octopus have been reported to carry a coconut shell and it was discussed as planning behaviour (Finn et al., 2009). However, one can argue that this behaviour is motivated by their current need to hide from predators. Our study provides the first experimental procedure aiming to test future planning while controlling for current motivational state in a cephalopod.

No significant effect of age was found. However, 80% of juveniles still chose the shelter arm the second day. We need to determine whether the 20% which chose the food arm, chose it at random or whether this was truly the reflection of planning behaviour. Some individuals in the juvenile group were older compared to other (i.e., 5 months old). They might possess more developed cognitive abilities than younger cuttlefish tested, allowing them to choose the shrimp arm by expressing future-planning behaviour. Indeed, the vertical complex which is the part of the brain involved in learning and memory in the cuttlefish is progressively maturing during the first three months after hatching (e.g., O'Brien et al., 2017; Dickel et al., 2001; Dickel et al., 2000). It would be interesting to do this experiment again with two homogeneous groups of juveniles: one group of cuttlefish with a mature vertical lobe complex (i.e., 5 months old), and one with an immature vertical lobe complex (2 months old).

Overall, our study provides the first preliminary evidence that cuttlefish can use past experience (i.e., access to shrimp at night when locked in the shelter arm), to take a decision in

the present (i.e., choice for the food arm), according to their future motivational state (i.e., future desire for shrimp) independently of their current motivational state (i.e., desire for shelter).

c. Neuronal substrates of episodic-like memory

In Chapter 4, we provided the first description of neuronal activations following an episodic-like memory task in the cuttlefish brain. More specifically, we showed a higher activation of the vertical lobe, the superior frontal lobe and the subvertical lobe in the trained group than in the control group (same sensory and motor stimulations, while not learning the what-where-when task). These lobes constitute the vertical lobe complex which is known to be involved in learning and memory in cuttlefish. Our study confirms previous findings showing the role played by the vertical lobe in learning and memory (e.g., Dickel et al., 2001; Sanders and Young, 1940; Graindorge et al., 2006; Shomrat et al., 2011). It brings also new data on the involvement on the superior frontal lobe (Agin et al., 2006) and the subvertical lobe in memory. Moreover, studies showed that the vertical-subvertical tracts were activated during memory processes and that degenerating fibres in these tracts were linked to impaired long-term memory performances (Dickel et al., 1997; Chichery and Chichery, 1992). Our study confirms and enlightens the role of the network involving these three brain structures, which may act in parallel to allow cuttlefish to solve the task. In humans, episodic memory is linked to a neuronal network comprising different brain structures (Rugg and Vilber, 2013; Fink et al., 1996). A well-studied structure of this network is the hippocampus which is known both for its central involvement in episodic memory and allocentric processing of spatial information (e.g., Burgess et al., 2002; Tulving and Markowitsh, 1998; Smith and Mizumori, 2006; Moscovitch et al., 2016; Shastri, 2002; Dolan and Fletcher, 1997; Eichenbaum, 2017; Miller et al., 2020; Sabariego et al., 2020). While remembering locations and context-dependent episodic memory involves the hippocampus, the link between these two roles of the hippocampus might be in the way it associates different features and builds relationships. In cuttlefish, the vertical lobe (i.e., one of the three lobes constituting the vertical lobe complex) is involved in spatial learning (Graindorge et al., 2006). Its involvement in an episodic-like memory task is then not surprising. However, our study is very preliminary and it remains to be determined whether the vertical lobe, which only receives pre-treated information *via* the superior frontal and the subvertical lobes, acts as the hippocampus: as a neural structure biding together different features of an episodic memory.

III. Comparison of episodic cognition in the common cuttlefish and the Eurasian jay and perspectives

This PhD thesis was created in a comparative perspective between the common cuttlefish and the Eurasian jay. More specifically, this work aimed at comparing their mental time travel abilities, involving episodic-like memory and its behavioural criteria (i.e., content, flexibility, and structure), future-planning, and source-memory. In this last part of the discussion, I will quickly compare cuttlefish and jay's capacities in these different domains, and present possible future work to go further in the investigation of MTT in these species.

Episodic-like memory

Evidence for content retrieval of episodic-like memories was already showed in jays prior to this PhD thesis (Clayton and Dickinson, 1998). It has also been showed that jays can flexibly retrieve the content of episodic-like memories (Clayton et al., 2003b), and build an integrated representation of these contents (Clayton et al., 2001b).

It has been evidenced that cuttlefish encode and retrieve the content of episodic-like memories (Jozet-Alves et al., 2013). In this PhD thesis, we demonstrated that cuttlefish can also use previous experiences to act flexibly in the present according to future conditions. However, no studies have demonstrated that cuttlefish behaviour in the episodic-like memory task answers to the third behavioural criterion of episodic-like memory, namely the structure (Clayton et al., 2003a). Indeed, it is not yet known whether cuttlefish can bind the what-where-when components into an integrated representation. Further studies should investigate this ability to validate all the described behavioural criteria for episodic-like memory in cuttlefish.

Crystal and Smith (2014) argue that when the memory load of an event is increased (i.e., this event presents a lot of features that we need to remember in order to differentiate it from other events), the subject can solve the task only by retrieving an integrated representation of this event. In other words, when two events are quite similar, the only way to discriminate them is to encode and retrieve specific features that characterize these events. In the literature, authors have manipulated the memory load of their subjects to investigate the structure criterion of episodic-like memory (e.g., Crystal and Smith, 2014; Clayton et al., 2001b). In the study of Clayton and collaborators (2001b), jays were first trained to learn that their preferred food was still edible after a short delay, but decayed after a long delay. Then, during the structure experiment, jays could cache mealworms in one side of a tray and peanuts in the other side of the same tray at day 1, and cache mealworms and peanuts again in a different tray at day 2

(mealworm in one side of the tray and peanuts in the other side of the tray). Four hours after the second caching period, jays could retrieve the food cached in the first tray, and after a short delay in the second tray. Contrary to the classic ELM task, mealworms were edible in the second presented tray and not in the first one. Thus, if jays had encoded the three components in an integrated representation, they should preferentially search for the peanuts in the first tray because the mealworms should be degraded whereas they should preferentially search for the mealworms in the second tray because they were cached 4 hours ago and are still fresh. Results confirmed this hypothesis showing that jays use a what-where-when integrated representation of the event. Similar results were found in chimpanzees using similar procedure (see Martin-Ordas et al., 2010).

To investigate whether cuttlefish have the ability to encode an integrated representation of what-where-when, we suggest using a similar overlapping features procedure. Cuttlefish would first learn that their preferred prey replenish after 3-hours but not after 1-hour (i.e. like in the original ELM task in cuttlefish, Jozet-Alves et al., 2013). Once they managed to perform the ELM training (i.e. they reach a learning criterion), cuttlefish would have the opportunity to perform the task in two different tanks. In one tank, the replenish conditions would be reversed: the preferred prey would be available after 1-hour and the less preferred prey after 3-hours (Figure 44a). In the other tank, the preferred prey would be available after 3-hours following the same replenishment rate than during the previous ELM training (Figure 44b). The two tanks

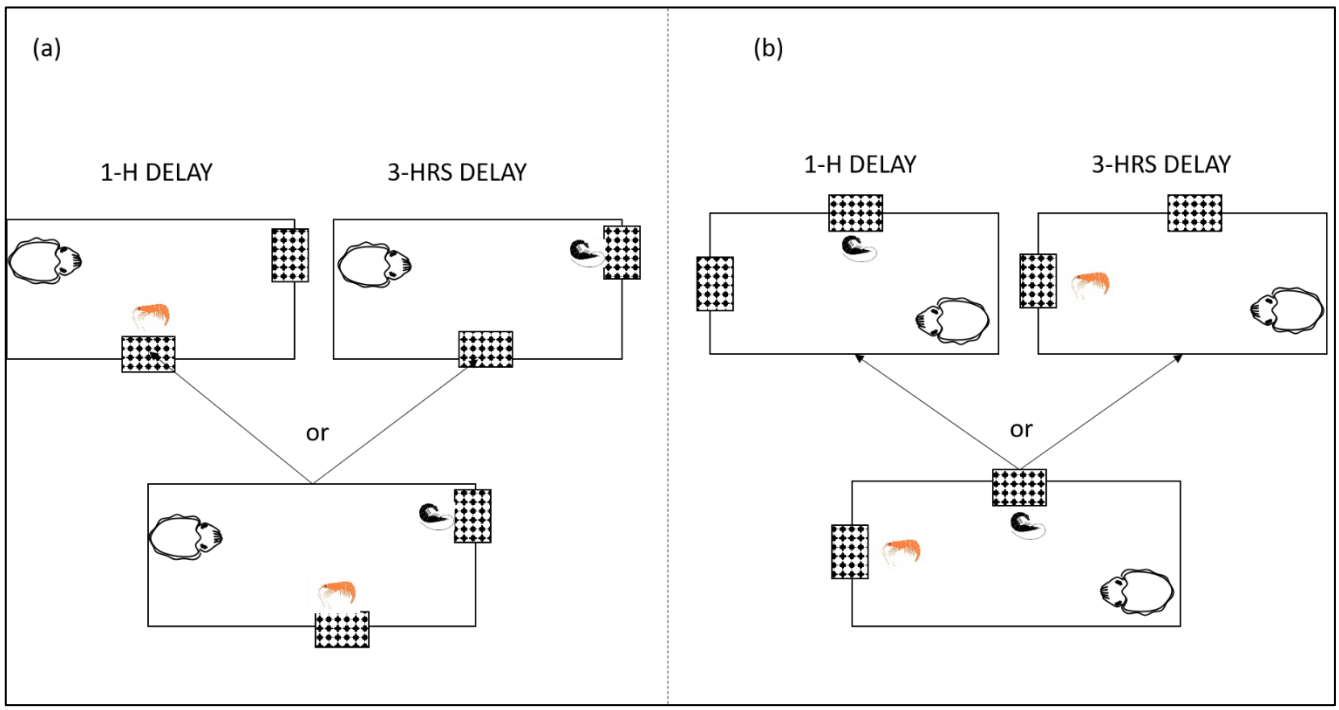


Figure 44 Imagined procedure for testing the integrated representation of what-where-when in cuttlefish.

would be the same colour and no external visual cue would allow the cuttlefish to distinguish the environments. However, the visual cues presented in both tanks would be presented at the different locations in the tanks (Figure 44). The location of the visual is changed every trial. If cuttlefish is able to encode a what-where-when integrated representation of the event, the where component should trigger the retrieval of what (type of food replenished or not) and how long ago the type of prey was encountered. Thus, in the first tank, cuttlefish should avoid going close to the visual cue associated with the less-preferred prey after 1-hour delay as they have learnt to do, but instead, go close to the visual cue associated with the preferred prey. They also should avoid going close to the visual cue associated with the preferred prey after 3-hours but instead, go close to the visual cue associated with the less-preferred prey. In the second tank, cuttlefish should go close to the visual cue associated with the less-preferred prey after 1-hour and should go close to the visual cue associated with the less-preferred prey after 3-hours like they have been trained to do previously.

Future-planning

It has been evidenced that Eurasian jays can plan for the future (Raby et al., 2007) independently of their current motivational state (Cheke and Clayton, 2012).

In this thesis, we showed that some cuttlefish can use previously encoded information to make a choice in the present according to the future. These results are preliminary, and further study will include a control group for the juveniles to ensure that their choice on day 2 is not due to random choice, and will involve a homogeneous group of juveniles (i.e., around the same age) to make sure that the results obtained is not due to differences in central nervous system's maturity. These limitations mostly concern juvenile cuttlefish. Results concerning adult cuttlefish capacity to plan the future are promising and the sample size will be increased to confirm or infirm our findings.

Source-memory

In this PhD thesis, we presented two new different ways to investigate source-memory in cuttlefish and jays. The source-memory investigation in cuttlefish showed that all cuttlefish were able to retrieve the source of the previously encountered item. The source-memory experiment in jays showed that males were able to retrieve a contextual source after incidental encoding, whereas females did not show this ability (for further discussion on the sex differences in this task see the part I. 2. Jays of the discussion).

Chapter 1 aimed at comparing the ability for source-memory in the common cuttlefish and the Eurasian jay. Using the same procedure in both species would have been a good way to raise the similarities and differences of both species performances in this task. For instance, jays could have been presented with different stimuli in different modalities (e.g., visual and auditory modalities). During training, jays would have the opportunity to learn to associate images with one perch, and sounds with another perch, and the absence of visual/acoustic stimulation with a third control perch (Figure 45a). Once jays would have reached a learning criterion, they would have been presented with a transfer test without delay, during which jays would be exposed to a picture or a sound not encountered during training (Figure 45b). When jays would have passed a transfer test without delay they would have been tested. During the transfer test with delay, jays would have been presented with a novel item either under visual or auditory modality (Figure 45c). At this stage, they would not have the opportunity to land on the perch associated with the modality of presentation of this item. Then, the item would be removed from the testing room. The perches associated with the visual and the auditory modalities would be placed in the testing room after a delay. If jays remember whether they heard or saw something before the delay, they would land on the perch associated with the modality of presentation of the item. This experiment would have been a first step to compare source-memory in both species. A second step would be to combine different features of the event in order to see whether jays and cuttlefish can retrieve several aspects of the memory and not only the perceptive modality in which the items are presented. For instance, we could

combine the retrieval of perceptual and contextual features (did I see or smell and in which spatio-temporal context?).

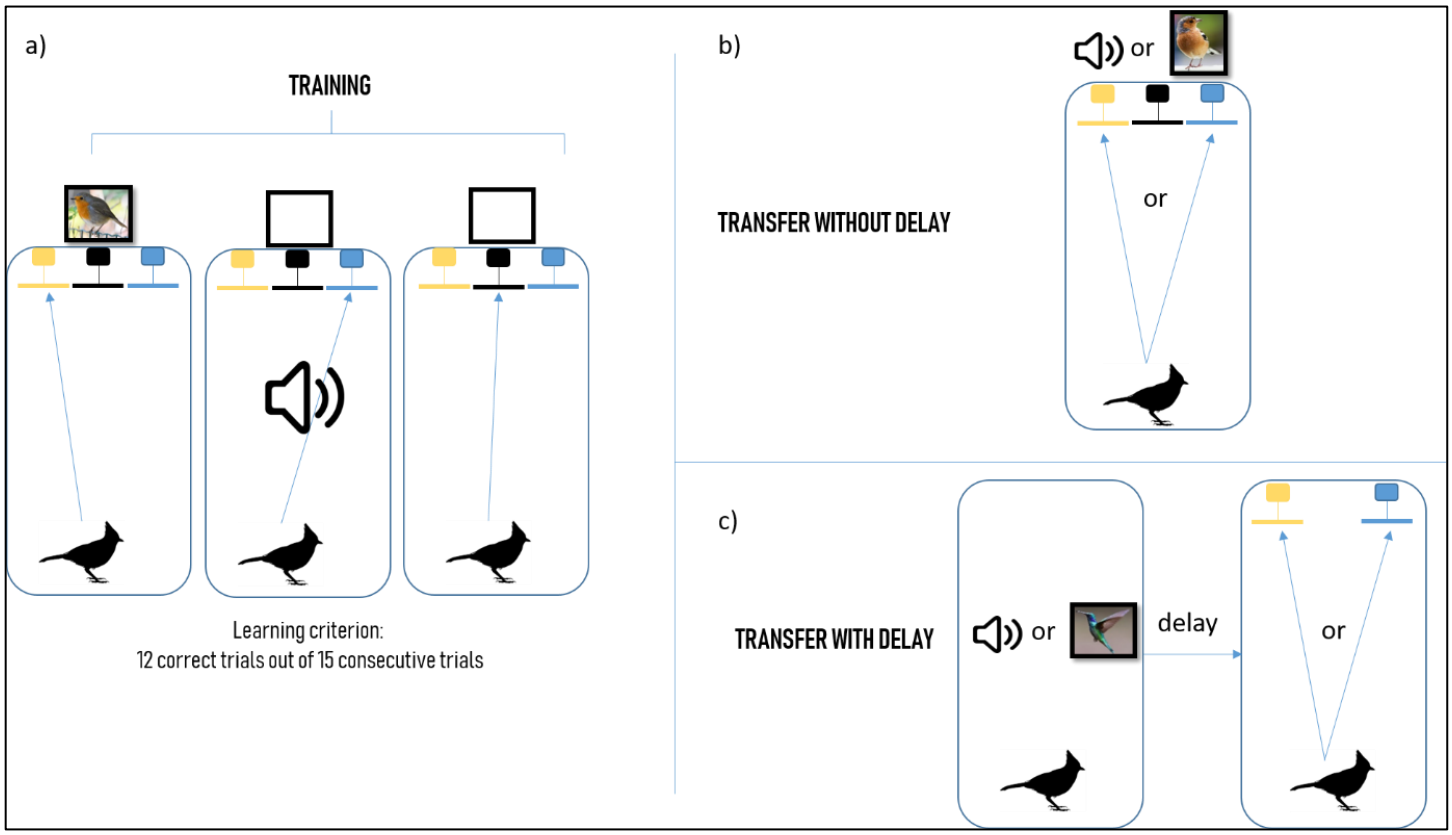


Figure 45 Imagined procedure for a source-discrimination task in jay reproducing the procedure used in the source-memory task in cuttlefish.

However, because the source-memory experiment in cuttlefish lasted one year, I decided to focus on the incidental encoding aspect of episodic memories in jays during my PhD. A step further would be to combine this incidental aspect with source-discrimination in cuttlefish. For instance, we could present cuttlefish with items under the visual or the olfactory modality in two different contexts which would be totally irrelevant for the task (e.g., different background contrasts or different luminosity levels). During training, cuttlefish would associate the modality of presentation of an item with a panel placed in the tank (i.e., one panel would be associated with the visual modality, another with the olfactory modality and the last one with no stimulation). While cuttlefish would perform this source-discrimination training, they would do so either in a high or in a low luminosity context (randomized across trials). Once cuttlefish would have reached a learning criterion and passed a transfer test without delay to make sure that they understood the general rule see *vs* smell, they would be tested. At test, 1) they would be presented with an item in the visual modality in a low luminosity context without having the opportunity to choose between the panels associated with the modality of presentation of the

item. After a short delay, the item would be removed from the tank and the luminosity would be back to normal. Then, 2) another item would be presented in the olfactory modality in a high luminosity context, without having the opportunity to choose between the panels associated with the modality of presentation of the item, after a delay the luminosity would be back to normal. 3) After a delay (long enough for the olfactory stimulation to be faded, according to water renewal rate), the luminosity would be either lowered again or highered and the two panels associated with the modality of presentation of items would be placed in the tank (Figure 46). The hypothesis is that if cuttlefish are able to retrieve in which modality the item was previously presented in presence of a low or high luminosity context, it means that they are able

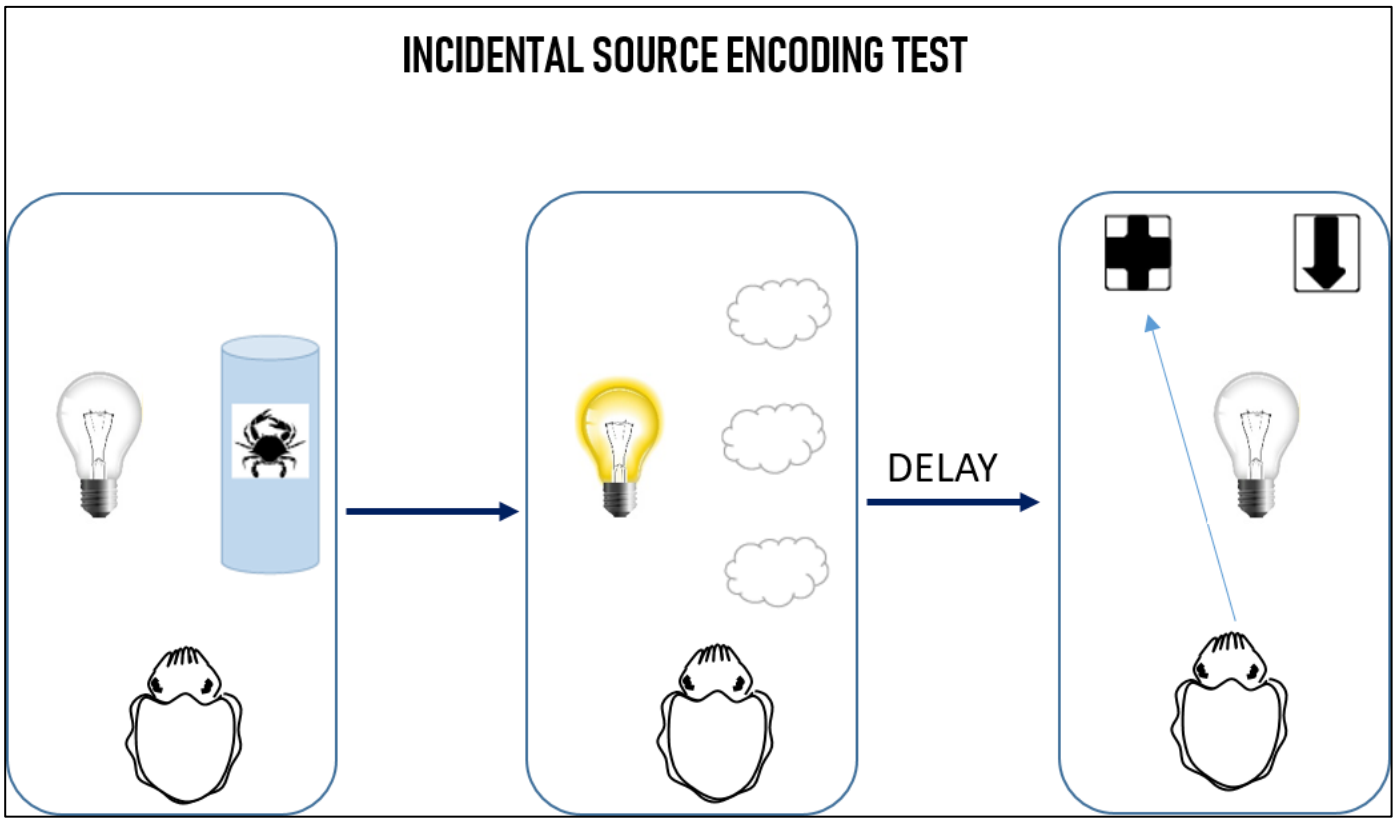


Figure 46 Imagined procedure for the incidental source encoding test in cuttlefish.

to retrieve the perceptive source of information from an incidental encoding of the luminosity context.

Ecological explanation of source-memory

The development of cognitive abilities in vertebrates has been explained ecologically in two hypotheses. The first postulates that complex cognition emerged to answer to the challenges of foraging and hunting for food (Ecological intelligence hypothesis, Byrne, 1997; Gibson, 1986; Janmaat et al., 2016). For instance, animals need to remember where and when they can

find food, based on previous experiences. The second postulates that complex cognition emerged to answer to the challenges of social demands of living with conspecifics (Social Intelligence Hypothesis, Schaik and Burkhart, 2011; Byrne and Whiten, 1988). For instance, animals need to remember the past episodes involving other conspecifics to interact with them accordingly.

Jays are vertebrates and the emergence of their complex cognitive abilities can be explained by the two hypotheses above. Indeed, jays present complex foraging cognition, with flexible food-storing foraging, and complex social interactions notably during breeding season. Their complex cognitive abilities might have evolved to answer to predation and social challenges. The complex cognitive abilities in jays and more generally in corvids led authors to postulate for a convergent evolution of these abilities in corvids and primates (Emery and Clayton, 2004).

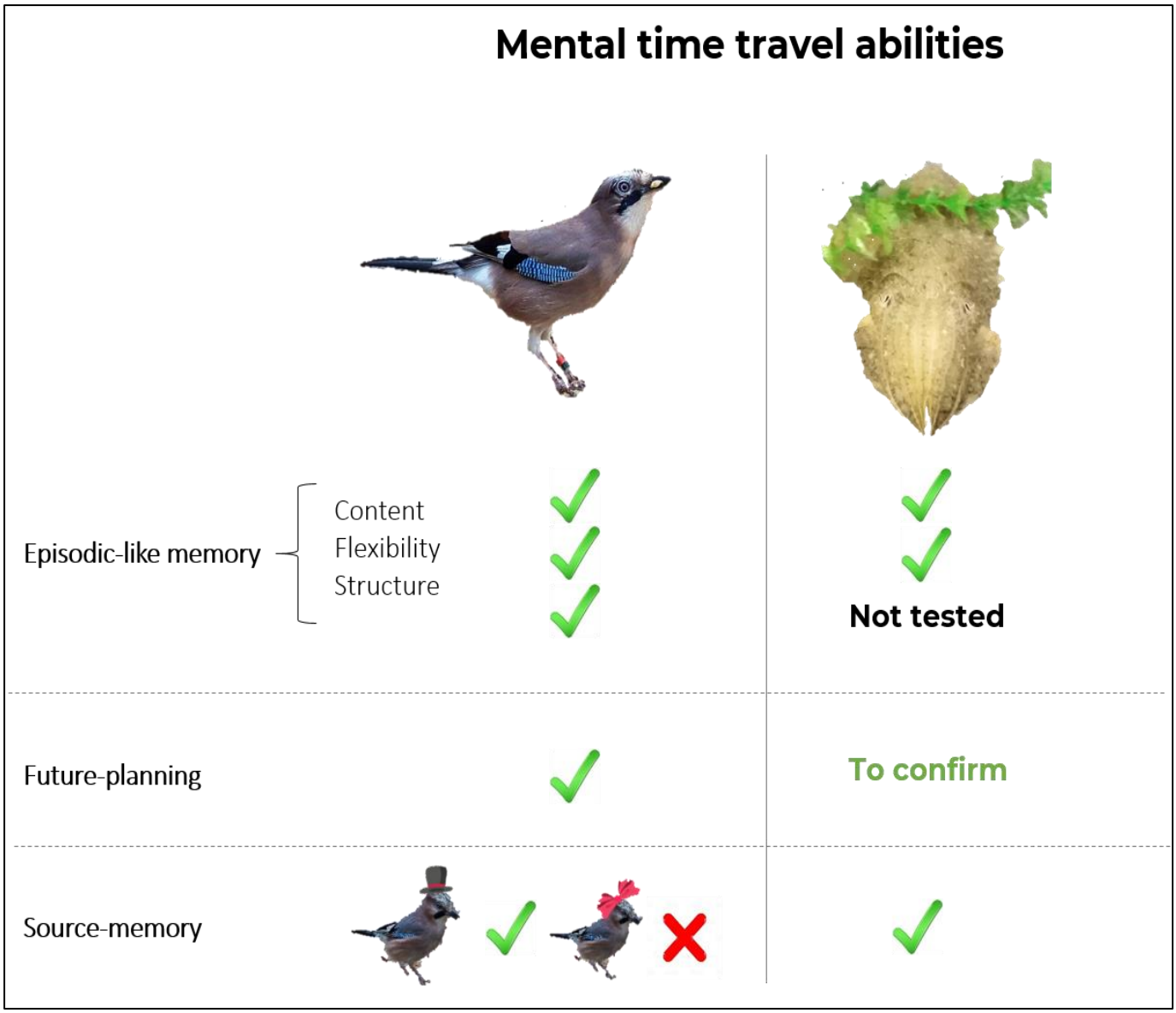
Cephalopods' cognitive abilities question the two hypotheses mentioned above because they evolve in a very simple social environment, and have very fast life histories. Recently, the question of the emergence of complex cognition was discussed in cephalopods (Amodio et al., 2019; Schnell et al., 2020). Authors argue that complex cognition would have arisen following environmental pressures due to the loss of their protective shell which have led cephalopods to spread in different environments and had to adapt to different and new environmental constraints, and in response to predation and social challenges due to mating processes. In this PhD thesis, we showed that cuttlefish were able to discriminate between their own perceptions, to retrieve them after three hours, to flexibly adapt their predatory behaviour, and we obtained encouraging results providing data on future-planning. Our work brings a new complex cognitive capacity to the list of the cognitive capacities that were shown in cephalopods (i.e., source-memory). The emergence of MTT capacities in cuttlefish could be the result of the strong environmental pressures due to the loss of the internal shell in cephalopods or to specific constraints encountered in the cuttlefish life history. Indeed, cuttlefish and octopus do not present the same defence tool-kit and do not have the same predatory behaviours (octopus can manipulate objects, break the shell of prey, etc).

The majority of discussion on the evolution of intelligence has focused on monkeys and apes because of their close relationship to humans. Investigating jays and cuttlefish in this PhD thesis brings new data which will be useful to compare the similarities and differences of

complex cognition between animal species, and which will be helpful to understand how these abilities have evolved.

Conclusion

To conclude, this PhD thesis bring new data on mental time travel in cuttlefish and jay suggesting that some features of episodic cognition might be shared by these species. This ability could have emerged under different environmental constraints, following foraging and predation constraints and/or social interactions. The ability to remember past episodes has been likely adaptive for the survival of the species, allowing them to find flexible strategies to face environmental changes and constaints. Whathever episodic-like cognition is similar to episodic cognition in humans, it seems that animals can definitely use previously encoded information



from single personally experienced events and use such information in the present according to the future.

Synthèse en Français

1. Introduction générale

Tel que nous en faisons l'expérience, le temps passe de manière linéaire, du passé vers le futur. Des auteurs de science-fiction ont imaginé des inventions extraordinaires permettant de voyager dans le temps avec peut-être l'espoir de les voir se réaliser un jour. Néanmoins, il est toujours impossible de voyager physiquement dans le temps. Ce qui est fait est fait. Comment, alors, pouvons-nous expliquer l'omniprésence du passé et du futur dans nos quotidiens ? Tous les jours, nous modifions notre passé, et nous agissons dans le présent en fonction de notre futur. Nous pouvons voyager dans le temps mentalement. Cette capacité de se projeter mentalement dans le temps est appelée « mental time travel » (MTT), et elle est discutée comme étant une capacité purement humaine.

Le voyage mental dans le temps peut être divisé en deux composantes : une composante rétrospective (voyage mental dans le passé) et une composante prospective (voyage mental dans le futur). Le versant rétrospectif est appelé « mémoire épisodique », définie comme la capacité de se remémorer des événements personnellement vécus. Ce type de mémoire fut d'abord décrite par Tulving (1972) en termes de relation spatio-temporelle (je suis capable de me souvenir de « où » et « quand » j'ai vécu ce moment particulier). Cette définition a beaucoup évolué au travers des années, et Tulving (2002, 2005) y a ajouté des éléments en termes de conscience : conscience du temps qui passe (je sais que je suis dans le présent, que mes souvenirs sont passés, et que demain est le futur), et conscience de soi-même (je sais que mes souvenirs sont les miens et que ceux des autres sont différents). Le versant prospectif est appelé « planification épisodique » et est intrinsèquement lié à la mémoire épisodique. Les deux versants ont longtemps été considérés comme indépendants. Aujourd'hui, les auteurs soutiennent que la capacité de se souvenir du passé personnel (mémoire épisodique) ne servirait en fait qu'un seul but précis : anticiper le futur (Schacter et Addis, 2007 ; Schacter et Madore, 2016).

Des êtres humains…

La capacité de voyager mentalement dans le temps est omniprésente dans nos quotidiens. Tôt dans le développement, on demande aux enfants ce qu'ils voudront faire lorsqu'ils seront grands, le week-end prochain, ou ce qu'ils ont fait à l'école (Martin-Ordas, 2016). Quant aux adultes, il est montré qu'ils parlent du passé ou du futur pendant plus de la moitié de leurs conversations (Szagun, 1978). Nos sociétés encouragent les individus à anticiper le futur et à se remémorer le passé. C'est le cas lorsque nous devons gérer un emploi du temps, une société, manager une équipe, ou tout simplement lorsque nous jouons à des jeux comme les échecs.

Le voyage mental dans le temps permet de reconstruire des épisodes passés, d'évaluer des situations présentes, et d'anticiper le futur. Lorsque cette capacité est altérée, notre capacité de comprendre le monde dans lequel nous vivons est également perturbée. Par exemple, des patients souffrant d'amnésie ne peuvent plus se souvenir de leur passé et ne peuvent plus reconnaitre leurs proches. Ces perturbations montrent à quel point la capacité de se souvenir et de se projeter dans le futur est importante pour nous, et participe à la création de notre identité personnelle (Corkin, 2002 ; Klein and Nichols, 2012).

...Aux autres animaux

Afin de survivre dans la nature, les animaux doivent apprendre et mémoriser des informations cruciales à partir de leurs propres expériences. Par exemple, les chatons doivent apprendre à attraper des proies, à grimper aux arbres, à s'auto-nettoyer, etc. Cette capacité d'apprendre et de mémoriser est cruciale pour que les animaux puissent s'adapter convenablement à leur environnement, et il y a un consensus global dans la littérature scientifique sur le fait que les animaux possèdent des capacités mnésiques (Kamil et Roitblat, 1985 ; Healy et Jones, 2002). Ce qui est débattu, par contre, est le type de mémoire que les animaux possèdent. Selon certains auteurs, les animaux ne pourraient pas comprendre le temps qui passe, et seraient toujours ancrés dans le présent. Ainsi, leurs capacités mnésiques se limiteraient à des capacités liées à l'apprentissage (apprentissage de règles leur permettant de résoudre des tâches par conditionnement) et les animaux ne possèderaient pas de capacité de mémoire épisodique. En d'autres termes, les animaux ne pourraient pas se projeter dans le passé afin de retrouver des informations ou se projeter dans le futur afin d'anticiper de futurs scénarios.

Pourtant, posséder des capacités de mémoire épisodique pourrait se montrer très adaptatif pour les animaux. Par exemple, retenir « où » et « quand » un type spécifique de proie

a été rencontré permettrait de sauvegarder de l'énergie lors de recherche de nourriture. Pour les oiseaux cachant leur nourriture, pouvoir retenir « où » et « quand » un type de proie en particulier a été caché permet de retrouver les proies qui risquent d'être périmées plus rapidement par exemple. Il a également été montré que les individus vivant en groupe auraient besoin de se souvenir de ce que les autres membres du groupe ont eux-mêmes vécu afin de pouvoir interagir de façon appropriée avec eux. Par exemple, si un jeune mâle se bat avec un mâle plus âgé et gagne le combat, les autres membres du groupe devront se souvenir que le jeune mâle est maintenant le dominant du groupe afin d'éviter des interactions belliqueuses.

Au cours des 30 dernières années, les chercheurs ont documenté les capacités de différentes espèces animales à se souvenir d'événements personnels ou à se projeter dans le futur. Même si l'avis des chercheurs défendant l'idée que le voyage mental dans le temps est unique à l'homme a quelque peu évolué, le débat autour de l'unicité du voyage mental dans le temps est toujours actuel. Cela est notamment dû aux difficultés de mesurer la mémoire épisodique avec des tâches non-verbales et d'interpréter le comportement des animaux au cours de ces tâches. Il est donc nécessaire de mesurer la cognition épisodique chez l'animal avec de nouvelles tâches non-verbales au niveau comportemental et cérébral afin d'apporter de nouvelles données à ce débat. Plus spécifiquement, l'étude de la cognition épisodique chez différentes espèces animales peut aider à comprendre comment cette capacité a évolué sous différentes contraintes environnementales.

2. Objectifs de la thèse

Le but premier de ma thèse de doctorat est de fournir de nouvelles données empiriques sur le voyage mental dans le temps chez l'animal. Ce travail est développé dans une perspective comparative pour mesurer différents aspects du voyage mental dans le temps chez un mollusque céphalopode, la seiche commune (*Sepia officinalis*), et chez une espèce d'oiseau, le geai des chênes (*Garrulus glandiarius*).

La seiche commune fait partie de la famille des invertébrés. Ces derniers ont été assez peu étudiés dans le domaine de la cognition complexe, et il n'existe aujourd'hui qu'une seule étude sur la capacité des seiches à pouvoir manipuler des informations épisodiques (Jozet-Alves et al., 2013). Afin de contrer ce manque de données, dans ma thèse, je vais étudier la capacité des seiches à répondre aux différents critères de la mémoire épisodique, comme la flexibilité. Comme la mémoire épisodique est maintenant discutée comme étant intrinsèquement liée à la planification épisodique, je vais également mesurer la capacité des seiches à anticiper le futur.

Ce travail de thèse vise à explorer un aspect de la mémoire épisodique qui a été très peu étudié chez l'animal : la mémoire de la source. La mémoire de la source est la capacité de récupérer en mémoire différentes informations du souvenir épisodique (par exemple des informations perceptuelles, contextuelles, affectives) afin de retrouver la source du souvenir (cela peut être : *qui* nous a dit cette information, *où* je l'ai entendu, si je l'ai *entendue* ou *lue*, etc ; Johnson et al., 1993 ; Mitchell et Johnson, 2009). La mémoire de la source sera étudiée chez la seiche en utilisant une nouvelle procédure expérimentale. Chez les geais, la mémoire de la source utilisera un aspect qui a été laissé de côté dans les études sur la mémoire épisodique chez ce groupe d'espèces d'oiseaux : l'apprentissage non-intentionnel. Les résultats obtenus à partir de ces deux études seront comparés. Contrairement à la seiche, de nombreuses études concernant les capacités de mémoire épisodique (e.g., Clayton et Dickinson, 1998) et de planification épisodique (e.g., Raby et al., 2007) ont été menées chez le geai. L'étude sur la mémoire de la source avec un apprentissage non-intentionnel viendra compléter la littérature scientifique existante en permettant de mieux comprendre la cognition épisodique chez cette espèce.

3. Organisation du manuscrit

Cette thèse est composée de quatre chapitres.

Chapitre 1 : CADRE THEORIQUE ET PRESENTATION DES MODELES

Le chapitre 1 présente une revue de la littérature sur le voyage mental dans le temps chez l'animal. Il inclut une première section sur la **cognition épisodique** qui comprend elle-même deux sous-sections : une première traite de la mémoire épisodique chez l'homme et chez l'animal dans une large variété d'espèces. La deuxième définit et décrit la mémoire de la source chez l'homme et comment elle est testée chez l'animal. Dans une deuxième section, nous parlerons de **l'étude comparative de la cognition épisodique**. Tout d'abord, je présenterai un rapide aperçu de l'histoire de la cognition comparée afin de mieux appréhender le cadre scientifique de ce projet. Ensuite, je présenterai les deux espèces animales étudiées au cours de cette thèse.

Chapitre 2 : EXPLORATION DE LA MEMOIRE DE LA SOURCE CHEZ LA SEICHE ET LE GEAI

Le chapitre 2 se concentre sur la mémoire de la source. Une première étude présente des résultats novateurs sur les capacités de la seiche à discriminer différentes source perceptives (i.e., modalité de présentation : source visuelle ou olfactive). Une deuxième étude présente une nouvelle façon d'étudier la mémoire de la source en mesurant les performances des geais à encoder de manière non-intentionnelle une information contextuelle (source contextuelle).

Chapitre 3 : EXPLORATION DE LA PLANIFICATION DU FUTUR

Le chapitre 3 présente deux études visant à étudier le comportement orienté vers le futur chez la seiche. Plus spécifiquement, la première étude a pour but de mesurer la capacité des seiches à anticiper la disponibilité de sa proie préférée le soir suivant et à modifier de manière flexible son comportement prédateur en fonction de changements environnementaux. La deuxième étude présente un nouveau protocole expérimental permettant d'étudier la planification épisodique chez la seiche.

Chapitre 4 : SUBSTRATS NEURONAUX DE LA MEMOIRE DE TYPE EPISODIQUE CHEZ LA SEICHE

Le chapitre 4 décrit une étude en immunohistochimie ayant pour but de révéler les marqueurs d'activation neuronale de la mémoire de type épisodique chez la seiche.

Tous les résultats obtenus au cours de cette thèse seront discutés dans la **discussion générale**. Les articles et le chapitre de livre parus dans des revues internationales sont insérés dans le manuscrit. Afin de faciliter la lecture de ce dernier, la numérotation des pages et des figures a été actualisée. Pour mieux faciliter la compréhension de chaque chapitre, ces derniers seront suivi d'un schéma récapitulatif des résultats principaux.

PREMIER CHAPITRE : CADRE THEORIQUE ET PRESENTATION DES MODELES

A. La cognition épisodique

I. La mémoire épisodique

Depuis l'antiquité, la mémoire fascine les intellectuels comme les philosophes, les artistes, les mathématiciens, et plus récemment les psychologues et les neuroscientifiques. La définition de mémoire a elle-même beaucoup évolué au cours du temps. Le 20^{e} siècle a particulièrement impacté l'étude de la mémoire. Sous l'influence de grands scientifiques tels que Bartlett (1886-1969), la mémoire n'est plus considérée comme une trace passive dans le cerveau, mais comme un processus actif de reconstruction d'événements passés. La mémoire humaine est divisée en plusieurs parties : la mémoire sensorielle (mémoire à très court terme et qui reçoit les informations sensorielles et perceptives captées par les sens), la mémoire à court-terme (stockage à court-terme de l'information) et la mémoire à long-terme (stockage à long-terme de l'information). Il fallut attendre la seconde partie du 20^{e} siècle avant de voir la mémoire à long-terme elle-même divisée en plusieurs types basés sur ses différentes fonctions.

On distingue deux grands systèmes de mémoire à long-terme qui diffèrent dans la façon dont les informations sont récupérées : le système non-déclaratif et le système déclaratif. Le système non-déclaratif concerne l'encodage et la récupération non-consciente de l'information. C'est ce type de mémoire qui caractérise les habitudes, les aptitudes procédurales comme faire du vélo, monter à cheval etc. Le système déclaratif, au contraire, est caractérisé par le rappel conscient de l'information. Les souvenirs déclaratifs sont donc rappelés consciemment, et parfois avec effort. Ces derniers peuvent être séparés en deux catégories : les souvenirs sémantiques et les souvenirs épisodiques. Les souvenirs sémantiques concernent les connaissances générales sur le monde (par exemple, Paris est la capitale de la France), tandis que les souvenirs épisodiques concernent les souvenirs personnellement vécus (ce que je portais et comment je me suis sentie lorsque je suis allée à Paris). La mémoire épisodique est la capacité de voyager mentalement dans le passé personnel. Les souvenirs épisodiques contiennent des informations contextuelles sur l'emplacement et la date du souvenir (i.e., quand et où l'événement s'est déroulé). La mémoire épisodique est aussi définie en termes phénoménologiques (de conscience). Cela veut dire que nous sommes capables de différencier les souvenirs des autres avec nos propres souvenirs, d'identifier nos souvenirs comme

appartenant au passé, que nous évoluons dans un espace temporel particulier (nous agissons dans le présent, nous nous souvenons du passé et anticipons l'avenir ; Tulving, 1983, 2002, 2005). Cette conscience s'appelle la conscience autonoétique qui englobe ce que Tulving appelle la Chronesthésie (conscience du temps qui passe, Tulving, 1983).

Cette définition en termes de conscience rend très difficile l'étude de la mémoire épisodique chez les animaux. En effet, les aspects phénoménologiques sont normalement étudiés à l'aide de tâches verbales où les participants témoignent de leur propre expérience subjective à propos de leurs souvenirs. Cette impasse a longtemps mené certains chercheurs à penser que la mémoire épisodique était spécifique aux humains. Néanmoins, depuis une trentaine d'années, la mémoire de type épisodique a été démontrée chez une large variété d'espèces animales (par exemple chez l'oiseau, Clayton et Dickinson, 1998, Gonzalez-Gomez, 2011, Zinkivskay et al., 2009 ; chez le rat, Babb and Crystal, 2006, Fortin et al., 2002, Belbidia et al., 2015 ; chez le campagnol, Ferkin et al., 2008 ; chez les primates, Martin-Ordas et al., 2010, Schwartz et al., 2005 ; chez le cochon, Kouwenberg et al., 2009 ; chez le chien, Fugazza et al., 2016 ; chez le poisson, Hamilton et al., 2016, chez l'abeille, Pahl et al., 2007 ; et chez la seiche, Jozet-Alves et al., 2013), et l'opinion des chercheurs a commencé à évoluer (Corballis, 2013).

II. La mémoire de la source

Afin d'approfondir nos connaissances sur la cognition épisodique chez l'animal, il est aujourd'hui nécessaire de l'aborder sous un angle nouveau. La mémoire de la source peut apporter cette nouvelle perspective. La mémoire de la source est la capacité de retrouver les éléments spécifiques qui composent un souvenir épisodique afin de l'attribuer à une source particulière (Johnson et al., 1993 ; Mitchell and Johnson, 2009). C'est une capacité essentielle dans notre vie quotidienne, qui nous permet de construire des jugements et des croyances sur le monde qui nous entoure (par exemple, cela peut être : décider si une information est fiable ou non, décider de retourner dans ce restaurant après en avoir gardé un bon souvenir, voir Mahr et Csibra, 2020 pour une revue sur le rôle crucial de la mémoire de la source chez l'humain). La mémoire de la source permet de créer une représentation mentale cohérente du passé afin de la ré-expérimenter mentalement (Moscovitch, 1994). A l'inverse, lorsque la mémoire de la source est impactée, des troubles mnésiques peuvent apparaître comme l'apparition pathologique de faux-souvenirs ou de confabulations qui peuvent handicaper profondément la vie de l'individu (Lindsay, 1994 ; Zaragoza et al., 2007 ; Loftus et Hoffman, 1989).

En 1993, Johnson et ses collaborateurs ont créé une modélisation du processus de récupération des différents éléments spécifiques composant le souvenir épisodique. Ils ont appelé ce modèle le « Source-Monitoring Framework » (SMF ; Johnson et Raye, 1981 ; 2000 ; Johnson, 2006 ; Lindsay, 2008 ; Johnson et al., 1993). Ce modèle illustre les mécanismes associatifs par lesquels les éléments perceptifs, contextuels, émotionnels, sémantiques liés au souvenir épisodique sont récupérés en mémoire. Ces éléments sont intégrés en une représentation cohérente, ce qui permet de visualiser le souvenir épisodique mentalement. Ensuite, cette représentation cohérente du souvenir est évaluée par des mécanismes décisionnels afin de déterminer la source du souvenir (Johnson et al., 1993 ; Mitchell et Johnson, 2009). Les auteurs distinguent plusieurs types de processus de récupération de mémoire de la source : le processus externe de mémoire de la source qui concerne la capacité de discriminer plusieurs sources externes à l'individu (par exemple, information entendue à la radio ou transmise par un voisin) ; le processus interne de mémoire de la source qui concerne la capacité de discriminer plusieurs sources internes à l'individu (par exemple, information pensée ou dite) ; enfin, le processus interne-externe de mémoire de la source qui concerne la capacité de discriminer une source interne et une source externe (par exemple information provenant de pensées ou d'événements vécus).

Lorsqu'un individu assiste à un événement, les éléments composants cet événement (aussi appelés signaux d'information) sont intégrés lors de l'encodage en une représentation cohérente de l'événement. Selon le niveau d'attention, le nombre et la qualité de ces signaux peut varier. Lors de la récupération, ces signaux vont être réactivés en mémoire. Plus le nombre de signaux encodés est important, et plus le nombre de signaux réactivés en mémoire est grand, plus la représentation mentale du souvenir sera claire. Lorsqu'un nombre suffisant de signaux peut être récupéré, la représentation mentale de la source de l'événement est facilement retrouvée : c'est ce qu'on appelle la recollection du souvenir épisodique. A l'inverse, lorsque les signaux du souvenir ne peuvent pas être réactivés, ou lorsqu'ils sont mélangés avec des signaux d'autres souvenirs, la source du souvenir ne sera pas automatiquement retrouvée. Dans ce cas, un sentiment de familiarité peut apparaître, et la source peut être retrouvée grâce à des stratégies cognitives liées à la prise de décision. Dans ce cas, les signaux encodés et retrouvés vont être évalués pour savoir s'ils constituent une représentation plausible de l'événement passé. Par exemple, vous pouvez avoir encodé une information mais vous ne vous souvenez plus qui vous a transmis cette information (est-ce que c'était votre collègue ou votre voisin ?). Afin de retrouver la source de l'information, vous allez évaluer la plausibilité de chaque source

en l'associant avec votre souvenir : si le souvenir implique un jardin, il est peu probable que l'information provienne de votre collègue, mais plus sûrement de votre voisin.

Il est important de noter que la mémoire épisodique et la mémoire de la source ne sont pas fondamentalement différentes (Johnson, 2005 ; Mitchell et Johnson, 2009). Au contraire, les deux sont intrinsèquement liées : d'un côté nous ne pouvons revivre un événement épisodique que si des processus de mémoire de la source sont activés. D'un autre côté, retrouver la source d'un événement implique de réactiver la mémoire épisodique de cet événement.

1. La mémoire de la source chez l'humain

Chez l'humain, la tâche classique pour étudier la mémoire de la source est la tâche « item *vs* source » qui a été largement documentée dans la littérature scientifique. Cette tâche oppose la capacité de retrouver un item (mémoire d'item) à la capacité de retrouver la source (ou le contexte) à laquelle l'item appartient (mémoire de la source ; Sprondel et al., 2011 ; Mitchell et al., 2006 ; Davachi et al., 2003 ; Jurica et Shimamura, 1999). Il est important de noter ici, que ce qui est référé au contexte dans la mémoire de la source comprend et dépasse ce qui est généralement appelé contexte dans la mémoire épisodique (i.e., le contexte spatio-temporel). En effet, le contexte dans la mémoire de la source indique tous les éléments qui étaient présents lorsque le souvenir épisodique a été formé (Mitchell and Johnson, 2009).

Pendant la phase d'étude de la tâche « item *vs* source », on présente une liste d'items aux participants comme par exemple : des mots (e.g., Elekes and Sebanz, 2020; Pergolizzi and Chua, 2016; Jeon et al., 2020, McCurdy et al., 2020), des images (e.g., Cycowicz et al., 2001; 2003; Petten et al., 2000), des visages (e.g., Lee et al., 2019), des voix (e.g., Glisky et al., 1995; 2001), des objets (e.g., Ventura-Bort et al., 2020; Stevenson et al., 2020), des formes visuelles (Slotnik et al., 2003), etc. Après un délai, pendant la phase de test, les items rencontrés précédemment sont mélangés avec de nouveaux items. Les participants doivent déterminer s'ils ont déjà vu ces items au cours de la tâche. Lorsqu'un item est considéré comme ayant déjà été vu, on demande aux participants de retrouver la source associée avec l'item (par exemple s'il appartient à des listes différentes, Wegesin et al., 2002 ; à des catégories sémantiques différentes, Gruber et al., 2008 ; dans quelle couleur il était présenté, Doerksen and Shimamura, 2001, etc).

2. La mémoire de la source chez l'animal

Très peu d'études se sont intéressées à la capacité des animaux à retrouver la source d'un événement. La preuve la plus frappante provient d'une étude sur le rat, où les auteurs ont développé un paradigme comportemental pour tester cette capacité (Crystal et Alford, 2013 ; Crystal et al., 2017 ; Smith et al., 2016 ; pour revue, voir Crystal 2016, Crystal, 2018). Dans leur première étude, les rats ont montré qu'ils étaient capables de discriminer des informations auto-générées (i.e., découverte d'un morceau de chocolat par eux-mêmes) et des informations générées par l'expérimentateur (i.e., l'expérimentateur a placé l'animal devant le morceau de chocolat ; Crystal et al., 2013). Pendant la phase d'étude, les rats étaient placés dans un labyrinthe radial, contenant des morceaux de chocolat distribués dans deux bras du labyrinthe de manière aléatoire. Les autres bras du labyrinthe contenaient des croquettes. Les rats pouvaient accéder aux morceaux de chocolat soit à l'aide de l'expérimentateur qui les plaçait directement devant les morceaux, soit par eux-mêmes, en explorant le labyrinthe. Si les rats trouvaient le chocolat par eux-mêmes pendant la phase d'étude, ce dernier était de nouveau disponible pendant la phase de test. Si les rats trouvaient le chocolat par le biais de l'expérimentateur, le chocolat n'était plus disponible pendant la phase de test. Les résultats ont montré que pendant la phase de test, les rats revisitaient significativement plus les emplacements où le chocolat avait été trouvé s'ils l'avaient découvert par eux-mêmes pendant la phase d'étude. Plus tard, les auteurs ont montré que ces résultats n'étaient pas dû à une erreur d'encodage où les rats auraient encodé seulement une partie de l'information et résolvant la tâche avec des processus associatifs (Crystal et Alford, 2014). Plus spécifiquement, les rats se rappelaient de la source de l'information après 7 jours.

La mémoire de la source a également été étudiée chez les primates. Dans une étude de type item *vs* source, les singes étaient capables de distinguer des images selon la tâche qu'ils avaient à faire (Basile et Hampton, 2017). Dans la première tâche, les singes étaient présentés avec une image sur un écran (e.g. un oiseau, un poisson, une fleur, une personne). Ils devaient toucher cette image afin d'accéder à l'étape d'après. Après un court délai, ils pouvaient classer la nouvelle image présentée en sélectionnant un des quatre symboles qui s'affichaient sur l'écran (chaque symbole étant associé avec une catégorie différente : oiseau, poisson, fleur, personne). Au cours du test de mémoire, l'image touchée, l'image classée, ainsi que deux distracteurs étaient diffusés sur l'écran. Quand les singes sélectionnaient l'image touchée, ils étaient récompensés avec de la nourriture. Lorsque les singes sélectionnaient une autre des images, un son négatif était diffusé. Dans la deuxième tâche, afin d'être certain que les singes n'avaient pas appris à sélectionner la première image présentée au lieu de discriminer les images

selon leurs sources, l'ordre d'apparition des images fut inversé. Dans la troisième tâche, la couleur de l'écran en arrière-plan changeait de manière aléatoire pendant la phase de test. Chaque couleur indiquait si le singe devait sélectionner l'image touchée ou l'image classée pour obtenir une récompense. Les singes ont réussi à sélectionner les images touchées même lorsque l'ordre d'apparition était inversé, et ils sélectionnaient de manière congruente l'image touchée ou classée selon la couleur d'arrière-plan proposée.

La mémoire de la source est liée à la mémoire épisodique. En effet, le rappel épisodique implique des processus de mémoire de la source. Une caractéristique qui définit la mémoire épisodique est que le souvenir peut être formé même lorsqu'il n'est pas encodé délibérément (Zhou et al., 2012 ; Zhou and Crystal, 2011 ; Singer and Zentall, 2007 ; Zentall et al., 2001 ; Zentall et al., 2008). Ainsi, une information encodée de manière non-intentionnelle ne peut être retrouvée que si elle implique des processus de mémoire de la source. Dans la plupart des études sur la mémoire de type épisodique chez l'animal, les individus sont entraînés à apprendre une règle. Ainsi, les individus entraînés peuvent former des attentes sur ce qu'il va leur être demandé. Par exemple, dans l'étude originale sur la mémoire de type épisodique chez les geais, les animaux étaient entraînés pour apprendre que les vers étaient toujours périmés après un délai long alors que les cacahuètes étaient toujours fraiches (Clayton et Dickinson, 1998). Les geais étaient entraînés et testés de la même façon : ils cachaient des vers et des cacahuètes, et après deux types de délais (un délai court et un délai long) ils avaient l'opportunité de chercher la nourriture cachée. Lorsque les animaux cachaient la nourriture, ils ont pu délibérément encoder l'information en vue du test de mémoire (Crystal, 2018 ; Singer et Zentall, 2007 ; Zentall, 2005 ; 2006 ; Zental et al., 2001 ; Zental et al., 2008). Ainsi, les animaux ont pu réussir la tâche sans se remémorer l'épisode passé mais en utilisant une règle sémantique.

Une solution pour ne pas que les animaux puissent résoudre une tâche en utilisant une règle sémantique, est d'utiliser un paradigme d'encodage non-intentionnel et/ou une question inattendue (Crystal 2013; Singer and Zentall, 2007; Zentall et al., 2001; Zentall et al., 2008; Zhou and Crystal, 2011). Lorsque l'information est encodée de manière non-intentionnelle, et lorsque les animaux ne savent pas qu'ils vont être questionnés sur une partie de la tâche, ils ne peuvent pas se référer à une règle délibérément apprise (Crystal, 2018). Le seul moyen pour eux de résoudre la tâche, est de retrouver mentalement l'épisode passé en utilisant la mémoire épisodique et la mémoire de la source (Singer and Zentall, 2007; Zentall et al., 2001, 2008; Zhou and Crystal, 2011).

La littérature scientifique a documenté l'utilisation de la question inattendue après un encodage non-intentionnel. Zentall et ses collaborateurs ont par exemple montré que les pigeons pouvaient retrouver un souvenir épisodique afin de répondre à une question inattendue (Singer et Zentall, 2007 ; Zentall et al., 2001 ; Zentall et al., 2008). L'encodage non-intentionnel et la question inattendue ont également été utilisé chez le rat (Zhou et al., 2012). Les animaux étaient entraînés à résoudre deux tâches dans le même labyrinthe composé de 8 bras en étoile. Dans une première tâche, pendant la phase d'étude, les animaux pouvaient se promener dans le labyrinthe afin de chercher de la nourriture dans 5 des 8 bras. Pendant la phase de test, les bras où la nourriture n'était pas disponible dans la phase d'étude étaient désormais ouverts avec possibilité pour les rats d'y trouver de la nourriture, tandis que les autres bras étaient fermés. Dans la deuxième tâche, les rats avaient accès à seulement 3 bras dans le labyrinthe, représentant un labyrinthe en T. Ils étaient placés dans un bras où ils pouvaient soit obtenir 6 croquettes de nourriture, soit pas de nourriture. Ensuite, ils étaient libres d'aller soit dans le bras de gauche soit dans le bras de droite. Ils étaient récompensés lorsqu'ils choisissaient l'orientation qui était associée avec la présence ou l'absence de nourriture dans le bras de départ (par exemple, tourner à droite signifiait présence de nourriture et tourner à gauche signifiait absence de nourriture). Dans une troisième tâche, les rats ont pu se promener dans le labyrinthe pour chercher de la nourriture dans 5 bras du labyrinthe (première phase de la première tâche). Ensuite, ils étaient placés de manière totalement inattendue dans le labyrinthe en T où ils pouvaient soit tourner à droite, soit tourner à gauche pour aller dans un des deux bras (deuxième phase de la deuxième tâche). Ainsi, les deux tâches étaient liées en une seule et même tâche. Les rats ne pouvaient pas savoir qu'ils devaient encoder la présence ou l'absence de nourriture dans la première tâche puisqu'ils n'étaient pas entraînés à le faire. Afin de choisir dans quel bras s'orienter (le gauche ou le droit) dans le labyrinthe en T, les rats ont dû encoder non-intentionnellement la présence ou l'absence de nourriture lors de leur recherche de nourriture dans les 5 bras du labyrinthe.

Souvent, dans les études présentant un encodage non-intentionnel chez l'animal, l'élément qui doit être encodé non-intentionnellement fait partie intégrante de l'entraînement, et l'animal doit se focaliser dessus pour réaliser la tâche. Dans ces études, il est possible que l'animal ait encodé l'information délibérément et pas non-intentionnellement. Ainsi, il serait nécessaire de proposer une nouvelle façon de tester l'apprentissage non-intentionnel chez l'animal, où l'information qui doit être encodée non-intentionnellement par l'animal n'est pas l'objet d'une attention délibérée. De cette façon, si l'animal est capable de retrouver

l'information encodée non-intentionnellement, cela ne pourrait se faire qu'à travers des processus de mémoire de la source.

B. Etude comparative de la cognition épisodique

Afin d'amener une vision comparative de l'étude de la cognition épisodique, j'ai choisi de me concentrer sur deux espèces animales très distinctes : le geai Eurasien (*Garrulus glandarius*) et la seiche commune (*Sepia officinalis*). Les geais sont le modèle de référence de la mémoire de type épisodique, cependant, certaines caractéristiques de la mémoire épisodique n'ont jamais été étudiées chez cette espèce. La seiche commune est le seul invertébré chez qui la mémoire de type épisodique a été démontrée (Jozet-Alves et al., 2013). Cependant, il existe un vrai manque dans la littérature scientifique afin de documenter si les capacités de mémoire de type épisodique des seiches remplissent les critères qui ont été déterminés pour pouvoir parler de cognition épisodique chez l'animal (Clayton et al., 2003a).

DEUXIEME CHAPITRE : EXPLORATION DE LA MEMOIRE DE LA SOURCE CHEZ LA SEICHE ET CHEZ LE GEAI

Introduction du chapitre : Ce chapitre présente deux protocoles afin d'étudier la mémoire de la source chez la seiche (*Sepia officinalis*) et le geai (*Garrulus glandarius*).

Article 1 / Partie 1 : Exploration de la mémoire de la source chez la seiche. Cette étude est inspirée des expériences de type item *vs* source chez l'humain. Les seiches avaient l'opportunité de retrouver des caractéristiques spécifiques associées avec un événement passé (des caractéristiques perceptives). Ces caractéristiques permettaient à la seiche de faire un choix entre deux sources perceptives différentes (visuelle ou olfactive), répondant à la question « l'ai-je vu ou l'ai-je senti ? ». Tout d'abord, les seiches étaient entraînées à discriminer des items visuels et olfactifs. Ensuite, lors d'un test inattendu, elles devaient se rappeler la modalité sensorielle dans lequel l'item avait été présenté précédemment (plusieurs heures auparavant). Nous avons fait l'hypothèse que si la seiche était capable de se rappeler dans quelle modalité les items avaient été rencontrés précédemment, alors qu'elles n'avaient pas été entraînées à répondre à la question après un délai, cela indiquerait l'implication de processus de mémoire de la source.

Article 2 / Partie 2 : Exploration de la mémoire de la source chez le geai. Dans cette deuxième étude, nous avons mesuré la capacité des geais à encoder de manière non-intentionnelle un indice visuel faisant partie du contexte. Les geais ont tout d'abord été entraînés à résoudre une tâche de discrimination simple au cours de laquelle l'indice visuel n'était pas impliqué, mais seulement présent en arrière-plan. Afin de résoudre cette tâche de discrimination, les geais pouvaient choisir de se percher soit sur un perchoir associé à des images d'oiseaux, soit un perchoir associé à des images d'arbres. Lorsque les geais réussissaient cette tâche de discrimination, on leur présentait un test de mémoire de la source inattendu. Au cours de ce test, les geais devaient se rappeler l'image qui leur avait été présentée en présence d'un indice visuel spécifique. Compte-tenu que les geais n'avaient pas appris à se focaliser sur cet indice visuel pendant l'entraînement, nous avons fait l'hypothèse que s'ils étaient capables de retrouver l'image qu'ils avaient vue en présence d'un indice visuel, c'est qu'ils l'avaient encodée non-intentionnellement et retrouvée grâce à des processus de mémoire de la source.

I. Exploration de la mémoire de la source chez la seiche.

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D'après le modèle de source-monitoring, l'origine d'un souvenir est retrouvée grâce à la réactivation en mémoire des traits qui composent ce souvenir. A l'aide de deux tâches de discrimination de la source, nous avons étudié la capacité des seiches à se souvenir de la modalité dans laquelle un item leur avait été présenté plusieurs heures auparavant. Dans l'expérience 1, les seiches ont montré qu'elles pouvaient retrouver la modalité de présentation d'un crabe (visuelle ou olfactive) 1h et 3h après sa présentation initiale. Dans l'expérience 2, les seiches étaient entraînées à retrouver la modalité de présentation de crevettes, de poissons, et de crabes. Après l'entraînement, les seiches ont passé la tâche une fois de plus avec un nouvel item que les seiches n'avaient jamais vu ou senti auparavant (par exemple, une moule). Les seiches ont réussi à passer ce test de transfert avec succès y compris après un délai de 3-heures. Cette étude est la première à montrer qu'un animal est capable de reconnaître et discriminer ses propres sensations. Pris ensemble, ces résultats suggèrent que la seiche peut retrouver les signaux perceptifs d'un événement passé, signaux visuels ou olfactifs.

II. Exploration de la mémoire de la source chez le geai Eurasien.

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En l'absence de critères comportementaux afin de mesurer les aspects phénoménologiques de la mémoire épisodique, il est toujours impossible d'établir si la mémoire de type épisodique est vraiment similaire à la mémoire épisodique chez l'homme. Un moyen innovant de tester la cognition épisodique chez l'animal, est de se concentrer sur un aspect crucial de la mémoire épisodique et pourtant quelque peu oublié dans les études chez l'animal. Cet aspect crucial est l'encodage non-intentionnel où l'expérience est encodée automatiquement. La plupart des études sur la cognition animale ont pré-exposé les animaux à l'élément qui devait être encodé non-intentionnellement. Ainsi, les animaux ont pu se concentrer sur cet élément et l'avoir encodé délibérément. Pour contrer cette limite, notre étude adopte deux nouvelles procédures : 1) une discrimination visuelle simple où un indice visuel est présenté en arrière-plan et est totalement inutile pour pouvoir résoudre la tâche et 2) un test d'encodage non-intentionnel inattendu mesurant la capacité des geais à encoder non-intentionnellement cet indice visuel. Pendant la tâche de discrimination visuelle, les geais étaient entraînés à discriminer deux types d'images en choisissant de se poser sur deux types de perchoirs colorés pour obtenir une récompense. Lors du test d'encodage non-intentionnel, les geais mâles étaient capables de rappeler quelle image ils avaient vue en présence de l'indice visuel. Les femelles, au contraire, semblent avoir choisi au hasard, alors qu'elles étaient plus rapides à apprendre la tâche de discrimination. Ces résultats inattendus suggèrent l'existence d'un dimorphisme sexuel dans la capacité de la mémoire de la source chez cette espèce.

TROISIEME CHAPITRE : EXPLORATION DE LA PLANIFICATION DU FUTUR

Introduction du chapitre : La littérature scientifique soutient que la mémoire épisodique sert à anticiper le futur (Schacter et Madore, 2016 ; Szpunar et al., 2014). En effet, retrouver un souvenir épisodique permettrait de construire un événement futur imaginé. Cette habilité d'imaginer des événements futurs basée sur des expériences passées, serait donc possible grâce à la nature reconstructive de la mémoire. Parmi les preuves que la mémoire épisodique servirait à la planification du futur, des auteurs ont par exemple montré que des réseaux neuronaux similaires seraient activés lors de la remémoration ou de la projection d'événements (Klen, 2013 ; Schacter et al., 2012). Ainsi, étudier les capacités des animaux à planifier le futur permettrait d'en apprendre plus sur leurs capacités de mémoire épisodique et notamment sur leur capacité de manipuler des informations passées de manière flexible.

Article 3 / Partie 1 : Comportement orienté vers le futur. Dans cette première étude, nous avons étudié les capacités des seiches à changer de manière flexible leur comportement prédateur en fonction des conditions environnementales changeantes. Lorsque les seiches savaient qu'elles allaient avoir des crevettes le soir (leur nourriture préférée), elles ont arrêté de manger des crabes dans la journée (leur nourriture non-préférée). Lorsqu'elles ne pouvaient pas prédire si leur nourriture préférée serait disponible le soir, elles ont continué à manger les crabes dans la journée. Enfin, les seiches étaient capables d'adapter de manière flexible leur stratégie de recherche de nourriture jour après jour en fonction des conditions expérimentales futures (présence ou absence de crevettes le soir).

Etude préliminaire 1 / Partie 2 : Exploration de la planification du futur chez la seiche. Dans cette seconde étude, nous avons mesuré la capacité des seiches à planifier le futur sans se baser sur leurs besoins présents. Le but de cette étude était de déterminer si une seiche pleinement repue choisirait un endroit où de la nourriture était disponible plutôt qu'un endroit avec un abri où elles savent qu'elles n'auront pas à manger pendant la nuit.

I. Comportement orienté vers le futur

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Certains animaux optimisent leur recherche de nourriture en apprenant et en mémorisant la disponibilité de leur nourriture en termes de quantité et de qualité, et peuvent adapter leur comportement en fonction. Dans cette étude, nous avons observé si les seiches pouvaient adapter de manière flexible leur comportement de recherche de nourriture à la disponibilité de leur proie préférée. Dans l'expérience 1, les seiches ont modifié leur stratégie de recherche de nourriture passant de sélective à opportuniste, lorsqu'elles ne pouvaient pas prévoir quand leur proie préférée allait être disponible le soir. Dans l'expérience 2, les seiches ont pu s'adapter jour après jour en modifiant leur comportement de recherche de nourriture en fonction de la disponibilité de leur proie préférée le soir même. Dans l'expérience 1, le nombre de crabes mangés (proies non-préférées) pendant la journée a fortement diminué lorsque les crevette (proies préférées) étaient disponibles tous les soirs. A l'inverse, la consommation de crabes pendant la journée s'est maintenue lorsque les crevettes étaient distribuées de façon aléatoire le soir. Lorsque les conditions étaient échangées, les seiches se sont rapidement adaptées à ce changement en modifiant leur stratégie de prédation en passant de sélective à opportuniste et vice versa. Dans l'expérience 2, les seiches ont réduit leur consommation de crabes pendant la journée lorsque les seiches pouvaient prédire que des crevettes seraient disponibles le soir. Nos résultats montrent que la seiche peut adopter un comportement prédateur très flexible incluant des stratégies sélectives et opportunistes en réponse à des changements environnementaux (présence ou absence de leur proie préférée le soir).

II. Exploration de la planification du futur chez la seiche

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Des auteurs soutiennent que les animaux ne peuvent anticiper leurs besoins futurs parce qu'ils ne peuvent pas se détacher de leurs besoins présents. Afin de remettre en question cette hypothèse, nous avons conduit une expérience avec 16 seiches juvéniles et 18 seiches adultes. Chaque seiche était testée dans un labyrinthe en Y où elles étaient nourries jusqu'à satiété. Ensuite, les seiches pouvaient choisir entre deux bras différents du labyrinthe : un bras où était placé un abri et un bras où étaient disponibles plusieurs crevettes. Après avoir fait leur choix, les seiches étaient enfermées dans le bras pendant la nuit et aucune nourriture ne leur était distribuée. Ainsi, les seiches qui avaient choisi le bras avec l'abri ne pouvaient pas manger de la nuit, tandis que les seiches qui avaient choisi le bras avec les crevettes pouvaient manger. Le jour d'après, après avoir été nourrie jusqu'à satiété une nouvelle fois, les seiches pouvaient de nouveau choisir entre le bras avec un abri et le bras avec des crevettes. Si les seiches étaient capables de prédire qu'elles n'auraient pas de nourriture pendant la nuit si elles étaient enfermées dans le bras avec l'abri, nous avons prédit qu'elles choisiraient le bras avec les crevettes. A l'inverse, si les seiches étaient ancrées dans le présent et ne pouvaient se détacher de leurs besoins actuels, nous avons prédit qu'elles choisiraient le bras avec l'abri. Toutes les seiches sauf une ont choisi l'abri le premier jour, un choix en accord avec leur besoin présent de se cacher dans le noir. Le deuxième jour, le bras avec l'abri n'était plus choisi préférentiellement par les juvéniles et les adultes. Un test contrôle a montré que les seiches étaient toujours attirées par le bras avec l'abri lorsqu'on leur proposait de choisir entre ce bras et un bras sans nourriture. Ainsi, cela suggère que les seiches n'ont pas choisi le bras avec les crevettes le deuxième jour à cause d'un renforcement négatif qui se serait opéré dans le bras avec l'abri pendant la première nuit (i.e., absence de nourriture). Même si cette étude est seulement préliminaire, elle présente la première procédure expérimentale pour étudier la planification du futur chez un céphalopode.

QUATRIEME CHAPITRE : SUBSTRATS NEURONAUX DE LA MEMOIRE DE TYPE EPISODIQUE CHEZ LA SEICHE

Introduction du chapitre : Dans ce chapitre, nous étudierons les substrats neuronaux de la mémoire de type épisodique chez la seiche. La mémoire de type épisodique a été largement étudiée chez l'animal, et un nombre croissant d'expériences supportent l'idée que les animaux peuvent se remémorer le passé. Les substrats neuronaux de la mémoire de type épisodique ont été étudiés chez les mammifères, et plus particulièrement chez les rongeurs. La recherche des substrats neuronaux de la mémoire de type épisodique chez la seiche enrichirait notre connaissance de la cognition épisodique chez l'animal. En effet, la seiche possède un système nerveux central bien différent de celui des mammifères. Mieux comprendre comment la mémoire de type épisodique est supportée dans le cerveau de la seiche nous permettrait de mieux appréhender l'évolution de la cognition épisodique. Dans notre étude, la protéine ubiquitin-c terminal hydrolase est utilisée pour étudier les activations cérébrales impliquées dans une tâche de mémoire de type épisodique chez la seiche.

I. Substrats neuronaux de la mémoire de type épisodique chez la seiche

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Les expériences de mémoire de type épisodique chez l'animal ont fourni la preuve comportementale que les animaux peuvent se souvenir de ce qu'ils ont rencontré précédemment, où et quand ils l'ont rencontré. La plupart des études se focalisant sur les substrats neuronaux de la mémoire de type épisodique ont été réalisées chez les rongeurs, et ont pour but d'améliorer notre compréhension des troubles de la mémoire épisodique engendrés par le vieillissement. Pourtant, explorer les substrats neuronaux de la cognition épisodique chez une espèce présentant un système nerveux central totalement différent de ceux des mammifères pourrait être utile pour mieux comprendre comment cette capacité a évolué. Les seiches semblent être un modèle d'étude prometteur pour cela, puisqu'elles possèdent des structures cérébrales bien distinctes de celles des vertébrés et elles représentent la seule espèce d'invertébrés chez qui la mémoire de type épisodique a été étudiée. Dans notre étude, 4 seiches ont été entraînées à résoudre une tâche de mémoire de type épisodique. Chaque seiche était couplée avec une seiche contrôle qui n'a pas reçu d'entraînement pour la tâche de mémoire de type épisodique. Une heure après avoir atteint le critère d'apprentissage de la tâche, le cerveau des seiches était prélevé. Nous avons étudié les activations neuronales du complexe vertical, une partie connue pour être impliquée dans l'apprentissage et la mémoire, en utilisant une nouvelle procédure neurobiologique : nous avons comparé les niveaux d'expression de la protéine ubiquitin-c terminal hydrolase (une protéine connue pour être un marqueur d'activation neuronale chez l'Aplysie) chez les seiches contrôles et chez les seiches entraînées. Les premières analyses ont montré une activation plus importante des différents lobes du complexe vertical chez les seiches entraînées en comparaison avec les seiches du groupe contrôle. Notre étude 1) apporte une nouvelle méthodologie pour explorer les substrats neuronaux de l'apprentissage et de la mémoire chez la seiche, et 2) est la première à explorer les activations cérébrales suivant une tâche de mémoire de type épisodique chez la seiche.

Conclusion

Pour conclure, cette thèse de doctorat présente de nouveaux résultats sur le voyage mental dans le temps chez la seiche et le geai en montrant que la cognition épisodique est sûrement partagée chez ces espèces. Cette capacité peut avoir émergé sous différentes contraintes environnementales, répondant aux contraintes de recherche de nourriture et de prédation et / ou aux interactions sociales notamment en période de reproduction. La capacité de se souvenir du passé a très certainement été adaptative pour la survie des espèces, leur permettant de trouver des stratégies flexibles face aux changements de leur environnement. Que la mémoire de type épisodique soit similaire ou non à celle des humains, il semble que les animaux puissent retrouver des informations encodées dans leur passé personnel et les utiliser dans le présent en fonction du futur.

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Etude Comparative de la Cognition Episodique chez la seiche commune (*Sepia officinalis*) et le geai Eurasien (*Garrulus glandarius*)

Résumé

Pendant longtemps, le voyage mental dans le temps a été considéré comme unique à l'humain. Selon des auteurs, les animaux ne pourraient pas se projeter dans le passé ou le futur parce qu'ils sont ancrés dans le présent. Néanmoins, pendant les 30 dernières années les chercheurs ont apporté des connaissances considérables sur les capacités des animaux à se souvenir de leur passé et à anticiper leur futur. Même si les opinions ont évolué, le débat sur l'unicité du voyage mental dans le temps est toujours d'actualité. Le but de ma thèse est d'apporter de nouvelles données sur les capacités des animaux à se souvenir du passé et à anticiper le futur. Plus particulièrement, je me suis intéressée à la mémoire de la source, qui est la capacité de retrouver l'origine d'un souvenir, chez deux espèces animales très éloignées, la seiche commune *Sepia officinalis*, et le geai des chênes, *Garrulus glandarius*. Les résultats ont montré que les seiches étaient capables de résoudre une tâche de discrimination perceptive, montrant qu'elles pouvaient discriminer et retenir leurs propres perceptions après un délai de 3 heures. Les geais, eux, ont révélé des différences mâles/femelles inattendues concernant leur capacité d'encoder et de retrouver une information contextuelle non-intentionnelle (source contextuelle). Une étude sur le comportement orienté vers le futur a montré que les seiches étaient capables de prendre une décision dans le présent en fonction de ce qu'elles avaient appris dans le passé, et en fonction des conditions expérimentales futures. Une étude préliminaire sur la planification a également apporté des résultats prometteurs sur la capacité des seiches à anticiper leurs besoins futurs. Enfin, nous avons pu explorer et mettre en lumière pour la première fois les substrats neuroanatomiques de la mémoire de type épisodique chez la seiche. Ces résultats permettent d'enrichir nos connaissances sur le voyage mental dans le temps chez la seiche et chez le geai, suggérant que cette capacité cognitive complexe peut avoir évolué sous différentes contraintes environnementales.

Mots-clés : Voyage mental dans le temps – Cognition épisodique – Planification – Cognition comparée – Seiche – Geai

Comparative Study of Episodic Cognition in Common cuttlefish (*Sepia officinalis*) and Eurasian jays (*Garrulus glandarius*)

Abstract

Some authors support that mental time travel is unique to humans. To their point of view, animals are not able to project themselves into the past of the future because they are bound into the present. Nevertheless, during the last 30 years, researchers have brought considerable knowledge on animals' capacities to travel mentally through time. Even though opinions have evolved, the debate concerning the unicity of mental time travel is still on. My PhD thesis aimed at bringing further knowledge on this matter by focusing on an innovative aspect of episodic cognition in common cuttlefish, *Sepia officinalis* and Eurasian jay, *Garrulus glandarius*, namely, source-memory. Source-memory is the capacity to retrieve the origin of an episodic memory. Results showed that cuttlefish were able to perform a source-discrimination study, revealing that they were able to discriminate and retrieve their own perceptions after 3-hours delay. A study on jays' capacity to encode incidentally a contextual information (contextual source) revealed unexpected differences between males and females. Investigation of future-oriented behaviour in cuttlefish showed that they were able to take a decision in the present according to previous encoded knowledge and according to future experimental conditions. A preliminary study also revealed promising results on cuttlefish capacity to anticipate their future needs. To finish, we explored and revealed for the first time the neuronal substrates of episodic-like memory in cuttlefish. Alltogether, these results provide new knowledge on mental time travel in cuttlefish and in jays, suggesting that this capacity would have evolved under different environmental contraints.

Keywords: Mental time travel - Episodic cognition – Planning – Comparative cognition –Cuttlefish – Jays