UNIVERSITÀ DEGLI STUDI DI PADOVA

DIPARTIMENTO DI BIOLOGIA

Corso di Laurea magistrale in Biologia Evoluzionistica

TESI DI LAUREA

Elements of episodic-like memory in the blue-headed macaw (*Primolius couloni)*

Relatore: Professore Andrea Augusto Pilastro

Dipartimento di Biologia

Correlatore: Dott.ssa Anastasia Krasheninnikova

Max Planck Institute for Biological Intelligence

Laureanda: Caterina Bonizzato

ANNO ACCADEMICO 2022/2023

Table of content

ABSTRACT

English version

Episodic memory is the "memory for personally experienced events" and can be defined as the property to process and store specific personal experiences, enabling individuals to relive episodes of their life that have taken place in a particular time and space.

Originally thought to be a unique characteristic of the human mind due to the lack of the appropriate non-verbal behavioural markers of consciousness for non-human animals, the body of data supporting that this memory system is indeed present across many different animal taxa is in constant expansion.

In this thesis, I provide data supporting that the blue-headed macaw, *Primolius couloni,* presents elements of episodic-like memory, therefore contributing to the first documented evidence that a parrot species does in fact rely on an episodic-like memory system to face different socio-ecological challenges.

Italian version

La memoria episodica è la "memoria degli eventi vissuti personalmente" e può essere definita come la capacità di elaborare e immagazzinare specifiche esperienze personali, consentendo agli individui di rivivere episodi della propria vita che si sono svolti in un determinato tempo e spazio.

Originariamente pensato come una caratteristica unica della mente umana a causa della mancanza di indicatori comportamentali non verbali di coscienza appropriati per gli animali, la quantità di dati a sostegno della presenza di questo sistema di memoria in molti diversi taxa animali è in costante espansione.

In questa tesi, fornisco dati a sostegno della presenza in ara dalla testa blu, *Primolius couloni*, di elementi di memoria di tipo episodico, contribuendo quindi alla prima prova documentata che una specie di pappagallo faccia effettivamente affidamento su un sistema di memoria di tipo episodico per affrontare diverse sfide socio-ecologiche.

1. INTRODUCTION

Memory is one of the most essential capacities for both humans and non-human animals, for instance, allowing individuals to remember specific locations linked to foraging or mating events, to build social relationships and networks with conspecifics, or, on the contrary, to avoid particular territories associated with rivalry episodes, hence enhancing the evolution of adaptive behaviours which allow the survival of many different taxa (Allen, et. al., 2013, Pause, et. al., 2013).

We can distinguish two types of memory systems that make up explicit (or declarative) long-term memory which is "implicated in the learning, representation and use of knowledge about facts ("semantic knowledge") and events ("episodic knowledge")" (Squire et al., 1992), Figure 1.

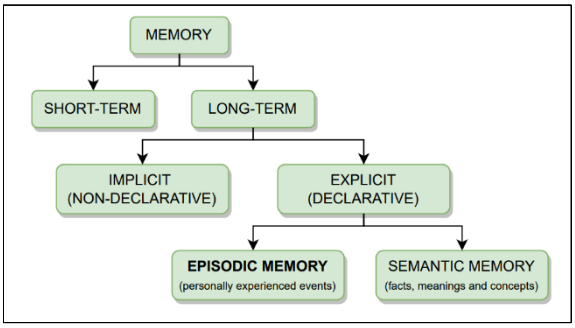

Figure 1: Memory systems.

While semantic memory refers to a general world knowledge involving facts, ideas, meanings and concepts that we have learned throughout the course of our life, which is not personal but which we shared between people of the same culture (Tulving, 1984, McRae et al., 2013; Saumier et al., 2002), episodic memory refers to the memory for particular personally experienced events situated in space and time. For instance, in semantic memory, we could store the general idea and description of what a cat is, as a small carnivorous mammal belonging to the Felidae family (i.e., small four-legged animal with fur, pointy ears, long tail, whiskers etc.), whereas, in episodic memory, we could store memory of the first time we petted our own cat, including where we were and at what time of the day that specific episode took place (i.e., experience episodically recalled).

Episodic memory is thus the "memory for personally experienced events" (Tulving, 1972) and can be defined as the property to process and store specific personal experiences, enabling individuals to relive episodes of their life that have taken place in a particular time and space. Tulving defined three key characteristics of episodic memory: a subjective sense of time (or "mental travel"), the connection to the self (or “self-awareness”), and an autonoetic consciousness (Tulving, 2002). In order to recall a specific episode in time, the ability to consciously perceive the passage of time is crucial, to say the least. Moreover, self-awareness becomes necessary since what we remember has been personally experienced by us: “no traveller, no traveling” (Tulving, 2002). Autonoetic consciousness refers to a special type of consciousness in which the act of remembering is accompanied by the “awareness that what is being remembered has happened to the self at an earlier point in time” (Gillund et. al., 2012). Other important aspects of episodic recall include visual and auditory imagery, narrative structure (Rubin et al. 2003), semantic information retrieval (Wheeler et al. 1997) and feelings of familiarity (Wagner et al. 2005, Hassabis et al., 2007).

Episodic memory contains summary records of particular experiences often represented through visual imagery that always has perspective. These memories are represented on a temporal dimension, roughly in order of occurrence, are autobiographical and are therefore recognized as experiences when accessed through processes of activation/inhibition patterns (Conway, 2009).

Finally, the purpose of the episodic memory is not only to enable individuals to encode and remember specific components of personally experienced episodes but also to actively use this information to potentially mentally time travel into the future, by making plans and predictions to deal with future challenges (Suddendorf et. al., 2009).

1.1 Episodic-like memory in non-human animals

For years, episodic memory was thought to be a uniquely human ability. Tulving argued that even if animals do present a very sophisticated and sensitive semantic knowledge of their environment, they cannot consciously recall and relive specific past experiences in the way humans can (Tulving and Markowitsch, 1998). Experimental protocols which aim to detect episodic memory in humans are however centred around language-based reports, directly asking subjects to episodically recall specific information. Yet, without any agreed upon non-linguistic behavioural markers, it becomes almost impossible to determine whether a non-human animal possesses episodic memory (Griffiths et. al., 1999). Clayton and colleagues were the first to argue that the retrieval and integration of information about "what, where and when" of a particular event, could be demonstrated experimentally in animals through their behaviour (Clayton, et. al., 1998, 2001). Clayton and colleagues (1998) showed that western scrub jays (*Aphelocoma coerulescens*) could remember not only the location (i.e., where) of two different food-caches (i.e., what), highly preferred but perishable wax worms and non-perishable peanuts, but also "adapt their caching and recovery strategies to the perishability of food stores" (i.e., when) (Clayton, et. al., 1998). Scrub jays searched preferably for fresh wax worms' caches after short delays following caching episodes but quickly switched to peanuts after long delays, learning their respective rate of perishability (Clayton, et. al., 1998). Given the evident impracticability of asking a non-human animal whether they consciously remember information of a particular experience, Clayton and colleagues argued that scrub jay reached the "behavioural criteria for episodic-like memory in non-human animals" (Clayton, et. al., 1998) and thus coined the term "episodic-like memory" which includes only the behavioural side of human episodic memory.

1.2 Evolution of episodic-like memory

Episodic memories in humans are formed and catalogued in the hippocampus, located in the temporal lobe, after the reception of information coming from the neocortex which is involved in sensory perception, generation of motor commands, spatial reasoning and language (Dickerson et. al., 2010).
Even though hippocampus and neocortex in avian species are not as well connected as they are in mammals (Rattenborg et. al., 2011), it is still clear that the hippocampus is indeed involved in the processing and storing of spatial information, contributing to the formation of episodic-like memories (Bingman et. al., 2005; Colombo et. al., 2000; Sherry, 2006). The visual and olfactory information elaborated by the avian brain, which reach the hippocampus, could still be sufficient for the formation of "what-where-when" memories for some bird species (Rattenborg et. al., 2011).

Allen and Fortin proposed that episodic memory has a long evolutionary history, as opposed to the hypothesis that it evolved relatively recently, solely in humans. They argued that the main characteristics of episodic-like recall are present in both mammals and birds and that the major brain regions involved in the formation of these memories in humans, could have anatomical and functional homologies in many different species, proposing that episodic-like memory depends on some fundamental neural circuits that are similar across both mammals and birds (Allen et. al., 2013). Considerable evidence shows that the circuit involving the hippocampus, parahippocampal region, and prefrontal cortex in the formation of episodic memory in humans presents a comparable counterpart across mammals and birds. This brought Allen and colleagues to hypothesize that "human episodic memory circuit shares an ancestral protoepisodic memory system with other mammals and possibly birds" (Allen et. al., 2013).

When talking about the evolution of episodic-like memory, it is essential to consider its adaptive importance and thus its contribution to individuals' fitness. Episodically remembering information of specific episodes happened in the past is not the only purpose of episodic memory; the significance of this memory system is to allow animals to think, reason, and plan for future events (Allen et. al., 2013). When faced with specific challenges, being able to recall components (i.e., what, where, when and who) of past experiences, enables individuals to make predictions and plans that best suits the challenge in question.

One main function of episodic memory can be found in the establishment of social relationships and networks. Being able to remember specific experiences linked with cooperation or aggression of other individuals, helps to process information during future social interactions, enabling individuals to better plan social interactivities with conspecifics. Recent evidence had also shown that humans which have episodic memory impairments, also have smaller social groups than individuals who do not have such impairments, suggesting that episodic memory could be crucial for the establishment and maintenance of social relations (Davidson et. al., 2012).

Other specie-specific functions of episodic-like memory are linked to the research of partners, for example by being able to predict when and where a sexual partner is sexually perceptive (Ferkin et. al., 2008) or linked to feeding strategies, by being able to remember and track the location, quality and replenishing rate of difference food sources (Clayton et al., 1998, González-Gómez et. al., 2011).

1.3 Different approaches and methodologies to study episodic-like memory.

There are two main paradigms to study the behavioural markers that could indicate the ability of non-human animals to episodically recall specific personal experiences: the "what-where-when" paradigm and the "incidental encoding and unexpected question" paradigm.

1.3.1 What-where-when paradigm

The what-where-when paradigm assesses whether an individual is able to remember a particular experience (i.e., what happened), together with the information regarding the location (i.e., where it happened) and the time in which this episode took place (i.e., when it happened). This approach requires a training phase prior to the testing phase in which the subjects need to learn a rule regarding the placement and the timing with which that particular episode will take place and shape their behaviour accordingly. For example, in the Clayton et al (1998) study, the scrub jays learned the respective perishability rate of different foods which became either unpalatable after a long delay (wax worms) or never perished, even after long delays (peanuts). This rule was learned through a "trial and error" training period and was used during the testing phase, in which scrub jays learned to visit trays in which they had previously cached wax worms after a shorter delay, while avoiding the same trays after a longer delay, preferring to visit trays in which they had cached peanuts. However, some authors argue that when subjects are trained for a long period of time on a specific memory task, they may solve the task by using semantic memory only (Singer, et. al., 2007, Zentall et. al., 2008, Zhou et. al., 2011, Zhou et. al., 2012).

1.3.2 Incidental encoding and unexpected question paradigm

On the contrary, the "incidental encoding and unexpected question" paradigm uses highly stringent test trials in which the subjects need to encode information about different components of a specific episode (i.e., "what and where" or "what and who”) incidentally. Afterwards, the subjects are asked “unexpectedly” to remember the encoded information.

Recently, Davies and colleagues (2022) showed evidence of episodic-like memory in eight common bottlenose dolphins using the “incidental encoding and unexpected question” paradigm. They tested each individual on two different memory tasks, dividing the experiment into a first “encoding phase”, in which the subjects had to incidentally encode information, and a second “memory phase”, in which they had to unexpectedly solve the memory task. In a “what-where” memory task, the subjects were tested on whether they remembered the location of an object (i.e., a toy ball) after the experimenter who gave them the ball in the “encoding phase” switched positions with another experiment who did not have any objects prior, therefore remembering the location (i.e., where) of the ball (i.e., what). In a “what-who” memory test, the dolphins were tested on whether they remember which of the two experimenters gave them the ball in the “encoding phase” after they had moved locations, therefore remembering which experimenter (i.e., who) presented them the ball (i.e., what).All subjects passed the “what-where” memory test and 7 out of 8 passed the “what-who” memory test, therefore showing evidence of episodic-like memory in bottlenose dolphins.

Despite the criticisms around the “what-where-when” paradigm, Holland and Smulders demonstrated how humans also use episodic memory even when instructed to actively remember information during the “encoding phase”, therefore expecting a memory test, which resembles what happens when non-human animals are trained repeatedly on memory tasks (Holland and Smulders, 2011). In this experiment, Holland and Smulders compared two groups, one subjected to a “passive treatment”, in which they were not asked to actively encode information, and another subjected to an “active treatment”, in which they were told to remember that information for a subsequent memory test.

Most of the participants reported using a mental time travel strategy to solve the task and their performance on the what-where-when test was significantly predicted by the performance on a different incidental encoding task, which suggested that not only the what-where-when memory task is a good test of episodic memory in humans, but also that both paradigms could be used together to support each other leading to more conclusive evidence of episodic-like memory in animals (Holland and Smulders, 2011).

1.3.3 Other approaches

Other approaches shift their focus to only two dimensions of episodic memory recalls at the time.
For example, in the “what-where” memory test, the focal point shifts to the special context of the episode: subjects are tested on their memory to the location of objects or odors, either in a physical space or on a specific location on a screen (Gilbert et. al., 2002, 2003, Day et. al., 2003, Rajji T, et. al., 2006, Gaffan, 1994). On the other hand, the “what-when” memory test, focuses on the temporal context in which specific episodes occurred. Subjects are tested either on the memory of the order in which events took place, on how long-ago events happened or on at what time of the day which event took place (Friedman, 1993, Roberts, 2002, Eichenbaum et. al., 2003).

After the pioneering work of Clayton and colleagues on western-scrub jays, many others have shown the display of elements of episodic-like memory in many different species (Lo et. al., 2019; Fugazza et. al., 2020; Babb et. al., 2006; Panoz-Brown et. al., 2016; Dere et. al., 2005; Roberts et. al., 1996; Schwartz et. al., 2001; Schwartz et. al., 2002; Davies et. al., 2022; Zentall et. al., 2001; González-Gómez et. al., 2011; Zinkivskay et. al., 2009; Feeney et. al., 2009; Pahl et. al., 2007; Jozet-Alves et. al., 2013, Schnell et. al., 2013). It has been therefore suggested that the elemental properties of episodic-like memory could be present across many mammal species, as well as in a number of birds and even invertebrates’ taxa.

Birds have often been overlooked in the comparative cognition field in the past, for instance being used merely as models for associative learning (Emery, 2006). Yet birds like corvids and parrots have frequently demonstrated their amazing cognitive abilities and are now been considered more as models for human cognition.

1.4 Birds as models for higher cognitive abilities: evolution of the avian brain

Birds have often been considered to be less intelligent than other vertebrates such as mammals, thought to be primarily creatures of instinct, able to only respond reflexively to environmental stimuli (Emery & Clayton, 2005). Nonetheless, in human society, it is a common practice to refer to a not particularly bright person as "birdbrain". Yet, in the last years, many birds have repeatedly shown cognitive abilities that match or exceed those of many mammals (Emery, 2005), while birds such as parrots and corvids have been continuously showing outstanding performances in many cognitive test batteries, performing quantitively and qualitatively better than other birds while competing with non-human primates (Emery & Clayton, 2004; Emery, 2005).

One of the main reasons why birds were thought to be less clever than mammals was because of the confusing terminology of birds' forebrain structures, leaving to believe that birds could not produce flexible and intelligent behaviours (Emery, 2006). Traditionally thought to derive from basal ganglia, therefore thought to be involved in behaviours linked to sexual behaviours, feeding strategies and maternal care (Reiner et. al., 1998), it is now known that the avian forebrain is mainly derived from the pallium, exactly like the mammalian neocortex (Jarvis et. al., 2005; Emery, 2005).

Similarly to great apes, Corvidae (corvids) and Psittacinae (parrots), which performances outstand those of many other bird species, are thought to have developed their superior cognitive abilities, because they had to face similar socio-ecological problems (Emery, 2005). Parrots, corvids and great apes live in complex social groups, have a long developmental period before becoming independent from their parents (Emery, 2005) and live in constantly variable environments (Emery, 2006). Living in complex, individualized social groups (Humphrey 1976; Dunbar 1998), being able to find food in the environment (Milton 1988), extract shelled or cased food (Gibson 1986) as well as being able to use, fabricate and manipulate tools (van Lawick-Goodall 1970) have been suggested to be important factors for the evolution of primate cognitive skills. Thus, we can infer that the same factors might have also critically influenced the evolution of birds' cognitive abilities (Emery, 2005).

Parrots and corvids also present forebrains that are relatively the same size as great apes as well as the highest brain/body slopes throughout all bird species. Parrots in particular present higher neuron density in the forebrain then great apes, having a higher significant neuron counts in this region (Olkowicz et al., 2016). High packing densities neurons has been linked to the development of enhanced cognitive abilities as it is likely to results in higher speed of information processing (Olkowicz et. al., 2016).
Although the fact that brain size could truthfully reflect the ability of animals to perform complex cognitive skills remains on debate (Striedter, 2005) it has been repeatedly shown that avian species with relatively large forebrains, such as parrots and corvid, are also the ones who display cognitive abilities that are comparable to the ones of large-brained mammals such as primates (Van Horik et. al., 2012).

Hyperinflated forebrains in birds and mammals are thought to have evolved independently multiple times throughout different lineages (Nomura et. al., 2017). Since the last common ancestor of parrots, corvids and great apes lived approximately 300million years ago, it has been suggested that the cognitive skills that these taxa have demonstrate in the last three decades of animal cognition studies, could have evolved by a process of convergent evolution, driven by the need to adapt to similar environmental and social challenges (Emery, 2006; Van Horik et. al., 2012).
Ksepka and colleagues proposed that the main driver force that influenced the first major shift in the expansion of Neoaves after the K-Pg mass extinction, was a significant decrease in body size, which outpaced the subsequent decrease in brain volume, therefore resulting in larger average brain volumes at a given body mass (Kepka et. al., 2020). After this first shift, the opposite patten can be observed, where birds started to increase their body size, outpacing the simultaneous increase in brain size. Similarly to mammals, this coincided with the shift towards carnivorous diets, which characterizes four basally diverging telluravian clades (Accipitriformes, Strigiformes, Falconiformes, and Cariamiformes) and it is likely driven by their preference in specific prey types (Kepka et. al., 2020).

In parallel to this shift, driven by predatory ecologies, a second shift toward higher slopes (i.e., bigger brains in respect to smaller body size) was observed in two major clades of Telluraves: Afroaves and Australaves. Subsequently, a further decrease in body size occurred Australaves' Psittaciformes (parrots) which achieved one of the highest inferred rates of brain-body evolution within Neoaves together with crows (Kepka et. al., 2020).

Because of their exceptional cognitive abilities and their high relative brain size, parrots and corvids have been proposed as avian models for human cognitive neuroscience (Clayton & Emery, 2015). Solely used as models for associative learning for years (Emery, 2006), birds such as parrots and corvids can be confounding models for many complex cognitive abilities such as perception, information processing, decision making, memory and mental time travel.

Corvids such as western-scrub jays have been shown to be interesting models for studying episodic-like memory, being able to remember specific "what-where-when" components of past experiences (Clayton et. al., 1998). Scrub jays have also displayed their ability of planning for future events and therefore possibly showing their capability of mentally time travel (Clayton et. al., 2003).

To date, literature on memory in parrots is especially scarce, yet in a recent study conducted by Torres Ortiz et. al. (2022), it was shown how a species of parrot, the blue-throated macaw (*Ara glaucogularis*), was able to remember their previously performed actions which shows that not only they are capable of mentally represent themselves but this ability happens to be a prerequisite for episodic-like memory, therefore implying that parrots could have evolved episodic-like memory alongside corvids.

Since corvids such as western-scrub jays (Clayton et. al., 1998) and magpies (Zinkivskay et. al., 2009) has been shown to present elements of episodic-like memory, and since parrots show comparable cognitive abilities, forebrain size, face similar socio-ecological challenges and undergo long developmental periods as corvids, I present the first attempt of observing elements of episodic-like memory in a species of parrots, the blue-headed macaw (*Primolius couloni*).

1.5 The objective

This study aims to obtain knowledge on the ability of blue-headed macaws, *Primolius couloni*, to episodically recall specific food rewarded episodes using the what-where-when paradigm.

The following two hypotheses will be tested:

1. The blue-headed macaw, *Primolius couloni*, will be able to solve the what-where-when task using episodic-like memory.
2. All individuals will perform better after training than before training.

2. Materials and methods

2.1 General methods

2.1.1 Subjects, housing and nutrition

I tested seven blue-headed macaws (*Primolius couloni*) Fig. 2, three males (Mars, Mercury and Saturn) and three females (Andromeda, Callisto and Neptune), all hatched in 2014 and one female hatched in 2013 (Himalia). All parrots were hand raised in the breeding station of the Loro Parque Fundación and housed in aviaries located at the Max-Planck Comparative Research Station in Loro Parque, Tenerife, Spain.


Figure 2: Neptune, a female specimen of Primolius couloni, housed at the Loro Parque in Tenerife Spain.

The birds were housed together in a semi-open indoor aviary (28.61 m^2) with ambient outdoor temperature and with access to an outside area with natural light.

Food was provided both in the morning at around 9 am and in the evening at around 5 pm and consisted of a mix of 1/3 vegetables and 2/3 fruits. The parrots had ad libitum access to water. They were fed an additional "Versele-Laga – Prestige – Loro Parque" seed mix in the evening. I weighed the parrots after every session to keep track of their weight and motivation, adjusting the amount of seeds and fruits if any of them resulted under or overweight.

2.1.2 Test room and experimental setup

The parrots' aviary was divided into three big rooms separated by two sliding doors (Fig.3). The experiment took place in one of these rooms (Figure 3, room c). The dimensions of the experimental room were 240x245 cm. The rooms are divided with mesh; therefore, opaque plastic slabs were used to cover two walls of room c to visually isolate it from the rest of the aviary.

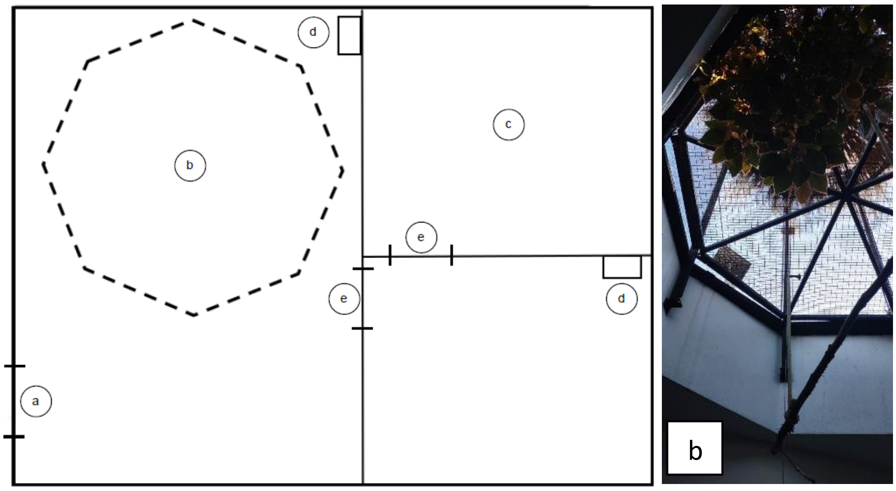

Figure 3: Aviary of the seven test subjects. On the left, a drawing depicting the general disposition of the rooms of the aviary. On the left a picture of the outside portion of the aviary that could be seen by the visitors of the park.

a. entrance, b. outside portion of the aviary, c. experimental room, d. food and water stations, e. sliding

As described in the figure 4ab, a table (1) of 145x163 cm, was placed in the centre of the room. The table was divided in 10 x 10 cm squares by using black tape as a grid (2): 12 columns, marked with a letter from “A” to “L” and 9 rows, marked by numbers from “1” to “9”.

Between the table and the experimenter, one curtain (3) was placed on a wooden frame (185x100 cm), which went from head height to arm height. The curtain separated the experimenter from the bird, in order to be able to prepare the setup whilst the bird waited until everything was ready, as well as to reduce any potential cues.

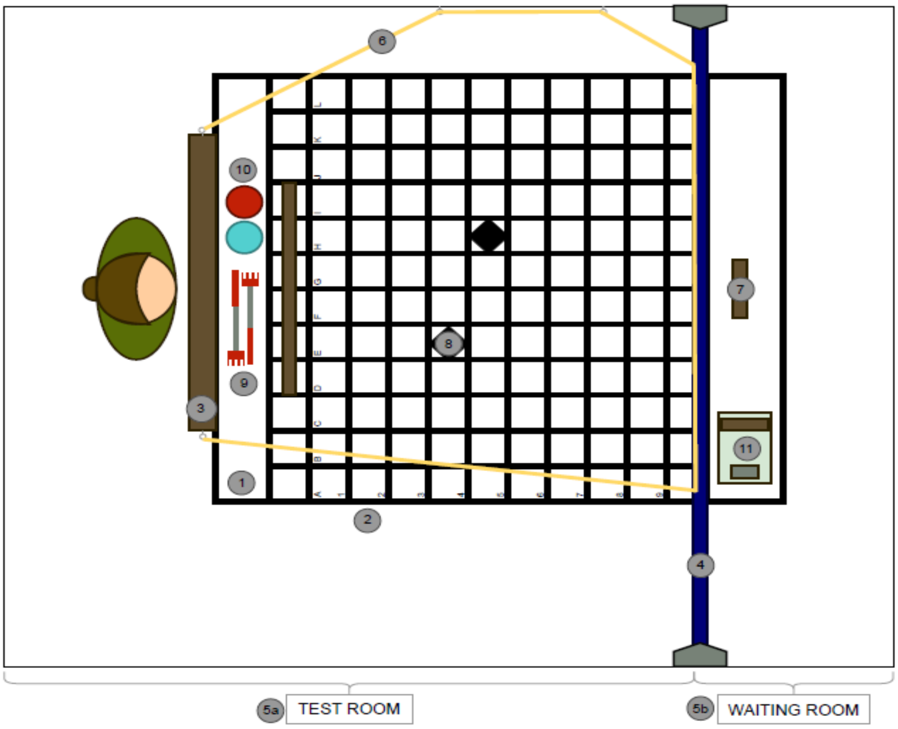

Figure 4a: Experimental setup.

Figure 4b: Experimental setup.

The curtain had a little square cut out covered with a plastic sheet, which served as a window so that the experimenter could be able to see the birds during the trial.
The window setup had a gap through which the experimenter was able to reach the table and manipulate the setup.

Another “separation wall” (4) (i.e., a 163 cm long curtain) was placed between the bird and the end of the table; the curtain divided the table into a “test room” (5a) which was approximately 7/8 of the table and a “waiting room” (5b), which measured the remaining 1/8s of the whole table.
The curtain was held using a metal rod and several plastic hooks.
The experimenter could open and close the curtain remotely using two ropes which were tied to the first hook and passed through all the others. The last hook was attached to one end of the metal rod in order to keep it in place while the separation wall was being manipulated.
In the “waiting room” a perch (7) was placed on the table, where each bird was asked to stay during the preparation of the trial, while in the “test room”, two wooden squares (8) (10x10 cm) with a smaller black square on a white background (stimuli, visual cues) were placed on two of the squares of the grid.
In order to be able to give the rewards (10) to the birds when they were not close enough for the experimenter to reach them, two extendable metal arms (9) were used.
In the centre of the two stimuli, two small magnets were glued on; allowing the experimenter to remove the stimuli after each trial, just by touching the magnets with the two extendable metal arms.

2.2 Habituation

2.2.1 Experimental room and set up habituation.

The birds were first habituated to the room, the table setup, the two curtains as well as to the stimuli and the extendable arms.

Once the opaque plastic slabs covered the two walls of the room and the table was placed in the room, the door was kept open for the birds to explore it for one day. From the next day, each bird was taken into the room individually and placed on the perch at the table with the door closed.

The first step of the habituation phase was to have, the birds exploring and walking on the whole surface of the table, while the separation wall was kept open.

Because the parrots were trained to follow a stick with a ball at the end of it and touch it with the beak, the experimenter encouraged the birds to explore the setup using this devise, and the parrots where reinforced using food rewards (mostly sunflower seeds as well as walnuts for an occasional bigger reward). The parrots were also clicker trained using operant conditioning, so they expected to get a reward once they heard the sound of the clicker.

In order to encourage them to explore the entire table, the experimenter moved the clicker around its whole surface, clicking and rewarding the bird every time it bit the clicker after walking around on the table.

The experimenter then proceeded to open and close the separation wall, first being together with the bird in the waiting room, with the help of a second experimenter who pulled the ropes and secondly, leaving the bird alone in the waiting room while the experimenter was in the test room.

After this first phase, the bird was placed on the perch behind the separation wall and it was presented with the stimulus.

The experimenter took one of the stimuli in their hand and showed it to the bird, clicking and rewarding it, therefore associating the new and scary object with something positive (i.e., a seed or a piece of nut).

When the bird felt more comfortable with the new object, the experimenter proceeded to bring the stimulus closer and closer to the bird, until it was possible to touch the beak of the bird with it, clicking and rewarding the bird. After a couple of times, the bird started touching the picture themselves to get the reward. The same exact procedure was carried out to habituate the birds to the extendable metal arms.

The experimenter then proceeded to train the parrots with two commands which were taught to all parrots (but Himalia) in previous experiments:

- The "Station" command: the experimenter says "Station!" indicating the perch with their extended arm while the bird is on the table. With this command the birds must climb on the perch in the waiting room and wait for the separation wall to close.
- The "Go" command: the experimenter says "Go!" in a characteristic high pitch voice, without indicating anything. With this command the birds are allowed to come off the perch and walk on the table to reach the stimuli (only used while the separation wall is open).

Once the birds felt comfortable with the setup and with the commands, it was possible to go through the next phase.

2.3 Preference test

2.3.1 Individual reward preference

For each individual bird, a food preference test between two types of food (walnuts and sunflower seeds) was carried out to establish each bird's food preference. The rewards had to be different but still comparable in satiability. Each bird was taken into the room after the habituation phase and was presented with two different rewards: a small piece of a walnut or a sunflower seed. If walnuts were preferred in the habituation phase, the birds received a quarter of a walnut during the actual training and test trials, whereas during the "individual reward preference" phase, they were allowed to eat only a quarter of a walnut during the whole session, which was cut into smaller pieces. Because nuts are a high-calorie food, giving each bird a quarter of a walnut for every trial would be too much.

Each bird was brought into the test room alone and placed on a weighing scale to check its weight. The experimenter then used the “Station” command so that the bird walked or flew on the perch and waited for further instructions while the experimenter went behind the curtains.
The two rewards were presented on the hands of the experimenter, one next to each other, changing randomly the location of each reward between the two hands. The two rewards were presented at the same time.
The experimenter opened the curtain, presented the two rewards and then used the “Go” command.

The birds were then allowed to choose only one of the two rewards. The moment after the bird had chosen one or the other, the reward which they did not choose was pulled out of their reach by the experimenter.
The experimenter then used again the “Station” command and, only after the bird walked back on the perch, the experimenter proceeded to close the curtains. The curtain was closed after every trial.
These choices were presented to each bird 10 times every day consequently over a period of 3 days.

After this period of time, the individual food preference was established and served for the following training phase, only if each bird reached the criteria of choosing the same reward 9 out of 10 times on the third day of the preference tests.

In the case of a bird not reaching the criteria within 3 days, this phase would have been prolonged until the bird reached the criteria.

2.4 Training

2.4.1 Pre-training: learning to approach the stimuli to retrieve food

One session consisted of 10 consecutive trials each day, throughout 6 to 8 consecutive days. For each session (i.e., day), the experimenter positioned only one of the two stimuli on the table. The location of the stimuli was randomized, for each trial.

To avoid side biases, the two types of reward were given to the birds randomly and counterbalanced for each side of the table.
At the beginning of each session, each bird was brought into the room and placed on the perch to wait for further instructions while the separation wall was closed. While the bird was waiting, the experimenter placed the stimulus following the randomization sheet and then proceeded to go behind the curtain.
Once everything was ready, the separation wall was opened and the experimenter used the “Go” command so that the bird could approach the stimulus.
All parrots needed to approach the stimulus within 5 cm in less than three minutes. The choice was considered correct once the birds touched or stepped on it.

Once the parrots made a choice, the experimenter used the clicker and presented the reward assigned with the extendable arm. After, the stimulus was moved out of reach with the extendable arm, the bird was sent back to the initial perch using the “Station” command and the separation wall was closed. Once the bird was on the perch and the separation wall was closed, the stimulus was re positioned and a new trial started.

These choices were presented to each bird 10 consecutive times every day over a period of at least 6 to 8 days while the bird felt more and more comfortable with getting closer to the stimulus as well as touching it.
The birds were trained until they reached the success criterion of at least 9 correct choices (i.e., stimulus touches) in 10 consecutive trials.

2.4.2. Training phase: replenishing time

The goal of this phase was to teach the parrots that their preferred food was replenished after a long delay (3 hours) but not after a short delay (1 hour). On the contrary, their non-preferred reward was available in both delays.

In the training phase, two identical stimuli were placed on the table in fixed positions for the whole duration of this stage, but the positions varied between the 7 birds, following the randomization sheets.

To sure that both stimuli (i.e., both rewards) were seen by the birds at the same time, I set the criteria for the stimuli of not being separated by more than three squares. Also, to avoid the parrots to reach both rewards, the stimuli needed to be separated for at least two squares. The stimuli could also be at different distances from the bird which will not differ for more than 2 squares (Fig. 5).

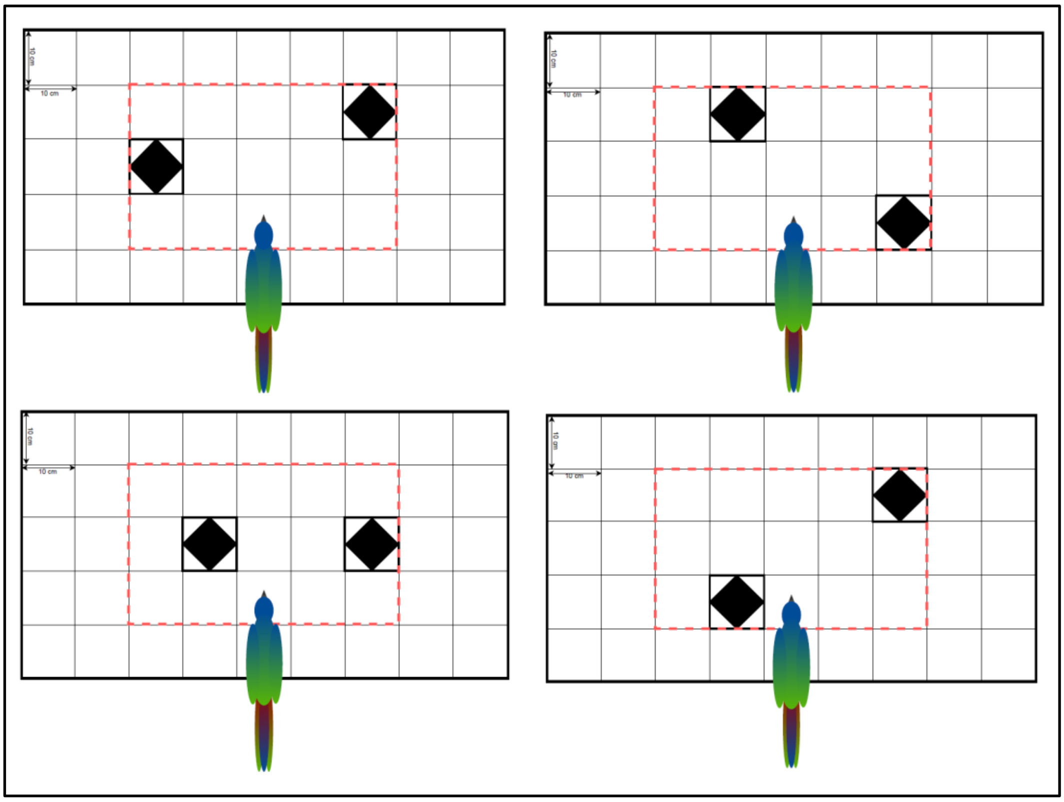

Figure 5: A few examples of the stimuli positioning on the table. The stimuli needed to be positioned inside of an imaginary 3x4 rectangle in which the stimuli needed to have at least a 2 squares distance between the two and not more than a 3 squares distance.

One stimulus was associated with the preferred food (i.e., walnuts), and the other was associated with the less preferred one (i.e., sunflower seeds).
The location of the two rewards remained the same for both stages of each session but changed pseudo randomly each day, so that the walnut, or the seed, could not be presented on one of the two sides (i.e., either right or left) more than 3 times in a row.

A trial consisted in two stages, a first stage before their feeding time (between 7:45am and 9:20am), where both rewards were present and a second stage either after 1 hour or after 3 hours, where the accessibility of the two rewards changed as stated above. Pictures from the recording of a session can be seen at page 33 (Figure 6).

Stage one: both rewards are presented to the bird

Each bird was brought to the room with the separation wall between the "waiting room" and the "test room" already closed and placed on the perch to wait for further instructions.
The experimenter placed the two identical stimuli on the table and then went behind the curtains. Then, the experimenter opened the separation wall and used the "Go" command for the bird to understand that it could come down the perch and approach one of the stimuli randomly. The parrots had three minutes to choose one of the stimuli once they were presented.
Once the bird had made its choice, the experimenter clicked and then presented the two rewards on their respective stimuli at the same time. The experimenter then proceeded to retrieve both stimuli rapidly using the extendable arm while still visibly showing the reward associated with the stimuli which was not chosen. The trial ended when the bird came back to the perch under the "Station" command, given by the experimenter and the separation wall was closed.
The bird was then asked to step on a weighing scale to check its weight and subsequently brought out of the room to switch with the next.

Stage two: 1-hour or 3-hour delay sessions

From here, each bird went through either a 1 hour-delay session or a 3 hour-delay session randomly.

1. **1-hour delay session:**

   In the 1-hour delay session, only the non-preferred reward (i.e., sunflower seed) was replenished, while the preferred reward (walnut) was not replenished.

   If the bird chose the stimulus whose position was previously assigned to the non-preferred reward, the experimenter clicked and the bird obtained the non-preferred reward. The experimenter also showed the empty arm in correspondence to the stimulus which was assigned to the preferred reward and then proceeded to retrieve both stimuli using the extendable arm.

   Otherwise, if the bird chose the stimulus which was previously assigned to the preferred reward, the bird did not receive any reward. The experimenter showed the first empty arm in correspondence to the stimulus which was assigned to the preferred reward and the second one, which will have a sunflower seed on top, in correspondence to the stimulus which was assigned to the non-preferred reward. The experimenter then proceeded to retrieve both stimuli using the extendable arm.

   The experimenter used the “Station” command and then proceeded to close the curtains.

   During this short delay session, the bird learned that only one of the stimuli corresponds to a reward and that that specific reward is their non-preferred one.

2. **3-hour delay session:**

   In the 3-hour delay session, both rewards were replenished in their respective stimuli.

   If the bird approached the stimulus which was previously assigned to the preferred reward, the experimenter clicked and the bird obtained that reward. The experimenter also showed the arm, which will have a sunflower seed on top, in correspondence to the stimulus which was assigned to the non-preferred reward and then proceeded to retrieve both stimuli using the extendable arm.

If the bird approached the stimulus which was previously assigned to the non-preferred reward, it obtained it. The experimenter also showed the arm, which had a quarter of a walnut on top, in correspondence to the stimulus which was assigned to the preferred reward and then proceeded to retrieve both stimuli using the extendable arm.

The experimenter used the "Station" command and then proceeded to close the curtains.

During this session, the bird was able to see how both stimuli lead to a reward and that the location of the rewards did not change throughout the trial.

The aim of this training phase was to teach the birds the replenishing time of the two rewards to see if they remember not only the location of the preferred-rewarded stimuli but also the timing in which the rewards are presented in the two delay sessions.

2.4.3. Criterion of success

The observer counted a trial as a "success" when the bird, after acknowledging the location of the two rewards in stage one, went directly to the non-preferred stimulus in the 1-hour delay session or to the preferred stimulus in the 3-hour delay session.

I took into consideration two types of correct sessions: a static session, where the bird chose the same side for both stages (i.e., 1-hour delay, seed-seed, 3-hour delay, nut-nut) and a switched session, where the bird switched the location choice between the two stages (i.e., 1-hour delay, nut-seed, 3-hour delay, seed-nut).

In the switched sessions, it is also possible to distinguish a higher value switch, where the bird had to choose the less preferred reward (i.e., sunflower seed) during the 1-hour delay trial, after it had chosen the preferred reward (i.e., walnut) during the first stage, and a lower value switch, where the bird chose the preferred reward during the 3-hour delay trial, after it had chosen the less preferred reward during the first stage (Table 1, 2).

The birds were trained until they reached the success criterion of at least 8 high-value switches in 10 consecutive switched sessions as well as 8 low-value switches in 10 consecutive switched sessions.

After the birds had reached this first criterion, I also took into consideration the static sessions which needed to reach a criterion of at least 8 correct choices in 10 consecutive static sessions while the switched session choices had to stay consistent while reaching this second criterion.

Sessions	**Definition**	**Types**
Static session	The subject chooses the same side for both stages	1h-delay: seed-seed
		3h-delay: nut-nut
Switched session	The subject switches their choice between the two stages	**High switch**, 1h-delay: nut-seed
		Low switch, 3h-delay: seed-nut

Table 1: Types of sessions.

Errors	Definition	Types
Static error	The subject switches their choice between the two stages erroneously	1h-delay: seed-none
		3h-delay: nut-seed
Switched error	The subject chooses the same side for both stages erroneously	**High switch error,** 1h-delay: nut-none
		Low switch error, 3h-delay: seed-seed

Table 2: Types of errors.

Lastly, if the subjects did not reach the criteria within 90 overall sessions, we considered them to have not learn the rule and would therefore pass to the testing phase to observe whether they would stay consistent and not pass the test or if daily changing the location of the stimuli would change the results.

2.4.4. Side bias correction

As parrots had been reported to develop strong side bias in previous experiments (Kim et al., 2009; Molina et al., 2019), we implemented side bias correction sessions after a bird had chosen the same side 4 days in a row.

Every bird went through a session of two trials every day, one for each stage; whenever a bird chose the same side 6 trials in a row (i.e., 3 days in a row), if during the first stage of the 4th day the bird chose the same side again (i.e., 7 trials in a row), the experimenter ended the session and started the side bias correction session.

After the choice, the bird was asked to go the station and the curtain was closed. The experimenter flipped the stimulus on the preferred side upside down and left the one which was not chosen facing up.
The experimenter then opened the curtain again and used the command “Go!”. After the bird chose the non-preferred stimuli, it received a small walnut piece as a reward; the bird was then asked to go the station and the curtain was closed. This procedure was repeated for 3 times, therefore reenforcing the choice.
After the third time, the experimenter proceeded to flip the preferred stimulus back, open the curtain and use the command “Go!”.

If the bird chose the preferred side again, it did not receive any rewards, it was asked to go to station and the experimenter flipped back the preferred stimulus to repeat the last step one more time. This procedure was repeated until the bird chose the non-preferred side.

If the bird chose the non-preferred side, it received a walnut piece as a reward and this step was repeated 3 times to make sure that the bird understood the correction. Only if the bird chose the non-preferred side for three times, then the side correction session was ended and the bird was brought outside of the room. After the side bias correction, the bird did not go through the second stage neither after 1 hour nor 3 hours.

The previous 3 days, as well as the side bias correction day, did not count during the analysis.

2.5 Testing phase

The birds were presented with the same process depicted in the training phase with the only exception that the location of the stimuli changed each day following a pseudo randomized sheet. As in the training phase, each bird was brought into the room and placed on the perch with the separation wall closed. The experimenter then proceeded to place the stimuli on the table according to the randomization sheet and then went behind the curtain. Afterwards, the experimenter opened the separation wall and used the "Go" command for the bird to approach the stimuli within three minutes.

Once the bird had made its choice, the experimenter clicked and then presented the two rewards on their respective stimuli at the same time. Then both stimuli were retrieved rapidly using the extendable arm while still visibly showing the reward associated with the stimuli which was not chosen. Lastly, the experimenter used the "Station" command and closed the separation wall.

The bird was then asked to step on a weighing scale to check its weight and subsequently brought out of the room to switch with the next.
From here, each bird went through either the 1-hour delay trial or the 3-hour delay trial pseudo-randomly and counterbalanced.
In the 1-hour delay session, only the non-preferred reward was replenished, while the preferred reward was not replenished, whereas in the 3-hour delay session, both rewards were replenished.

The observer counted a trial as a "success" when the bird, after acknowledging the location of the two rewards in the first stage, went directly to the stimulus assigned to the non-preferred reward in the 1-hour delay session and to the stimulus assigned to the preferred reward in the 3-hour delay session.
The birds were tested for 15 days. The success criterion for passing the test was kept at 80% (i.e., at least 12 correct choices in 15 sessions.)

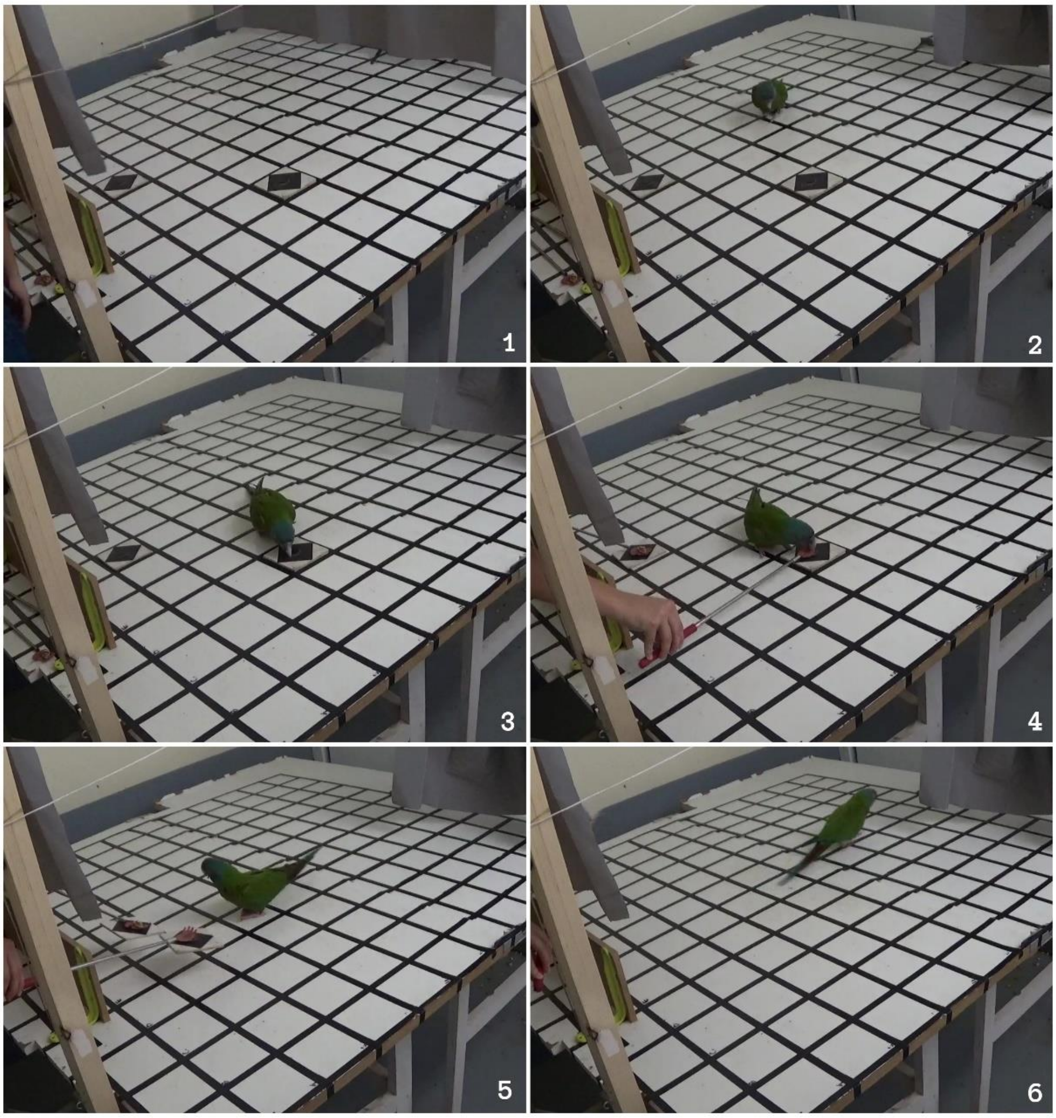

Figure 6: Phases of a session: 1. start of the trial, 2. opening of the separation wall, 3. subject chooses a visual cue, 4. subject is rewarded with the corresponded reward 5. subject is been shown the other reward corresponding to the visual cue it did not choose, 6. subject goes back to station

3 DATA ANALYSIS AND RESULTS

3.1 DATA ANALYSIS

For the analysis I used the program RStudio Version: 2022.12.0+353, released date: 2022-12-15.

I first analysed the video recordings of each individual to assess whether they passed the two criteria for both the training phase and the testing phase. Subsequently, I analysed first the performance of the whole group in its entirety using a repeated-measures linear model, in order to see if they improved or worsen their performances after the training periods, and secondly I analysed for each individual, whether their performance improved after training, comparing the first 15 days of training with the 15 days of testing, and whether their performance stayed consistent from the end of the training through the testing phase, comparing the last 15 days of training with the 15 days of testing, using single paired t-tests.

3.2 RESULTS

3.2.1 A word on the food preference test

With multiple combinations of seeds, nuts and fruits, after 13 days of testing, the best combination of rewards was walnut, as the preferred reward, being chosen 9 times out of 10 for 2 days in a row, and sunflower seed, as the less preferred reward, being chosen 1 time out of 10 for 2 days in a row.

3.2.2 Training

Three individuals out of 7 passed the training criteria. Mars (male, 9 years old), Callisto and Neptune (females, 9 years old) passed all three criteria for the training phase, correctly performing 8 correct static choices out of 10 static sessions (in 37, 36 and 56 sessions, respectively), 8 correct high switches out of 10 high switch sessions (in 74, 45 and 63 sessions, respectively) and 8 correct low switches out of 10 low switches sessions (in 75, 80 and 72 sessions, respectively).

One subject, Himalia (female, 10 years old), only passed two out of three criteria, correctly performing 8 correct static choices out of 10 static sessions, within the 72nd session, 8 correct low switches out of 10 high switch sessions, within the 51st session, but did not reach the high switch criteria within the 90th session.

One subject, Andromeda (female, 9 years old), only passed one out of three criteria, correctly performing 8 correct static choices out of 10 static sessions, within the 33rd session, but did not reach the high switch criteria nor the low switch criteria within the 90th session.

Two subjects, Saturn and Mercury (males, 9 years old) did not pass any of the three criteria within 77 and 62 sessions respectively, and since they would not have been able to pass the criteria within the pre-set session limit (i.e., 90 sessions) I therefore decided to test them nonetheless and to group them together with Himalia and Andromeda in the "Not-passed" group, in order to compare it to the "Passed" group, which included Mars, Callisto and Neptune as showed in the table below (Table 3) .

Name	Static criterion	High switch criterion	Low switch criterion	Group
Mars	✓	✓	✓	PASSED
Mercury	X	X	X	NOT PASSED
Saturn	X	X	X	NOT PASSED
Callisto	✓	✓	✓	PASSED
Neptune	✓	✓	✓	PASSED
Andromeda	✓	X	X	NOT PASSED
Himalia	✓	X	✓	NOT PASSED

Table 3: Training phase results.

Overall, the static criterion was the easiest one to reach, being reached by 5 subjects out of 7, followed by the low switch criteria, being reached by 4 subjects out of 7, while the hardest criterion to reach was the high switch criteria, being reached only buy 3 subjects out of 7.

3.2.2.1 Change of experimenter

Three subjects, Mars, Mercury and Saturn were both trained and tested by the same experimenter. Because of the prolonged timing of this project, the first experimenter was not able to conclude the testing with all the subjects. Three female subjects, Neptune, Callisto and Himalia, started testing with the first experimenter and then switched to two different experimenters. Andromeda finished training with one of the two experimenters cited above, and lastly, all four females switched to the last experimenter which concluded the testing phase.

Subsequently to these changes, I observed that the performances of the four females worsened relatively quickly. Especially Neptune and Callisto, which did indeed pass the training criteria, started to choose the visual cues randomly, without considering the information regarding the nature of the two rewards (i.e., what), their location (i.e., where) and the replenishing time rule (i.e., when) which they seemed to have learned during the training phase. I therefore decided to include a re-training period for all of them in order to give them a further chance to reach a reduced success criterion (i.e., at least two static sessions, two high-switch sessions and two low-switch sessions). Within the first month of this re-training phase, I noticed that none of them were reaching the criteria and I therefore decided to test them nonetheless, therefore eliminating the two groups, “passed” and “not passed”.

In the end, the data which were collected by the last experimenter were analysed as their last 15 days of training, after giving all 4 subjects a fair habituation period to that last experimenter during a re-training phase.

3.2.3 Hypothesis one: The blue-headed macaw, *Primolius couloni*, will be able to solve the what-where-when task using episodic-like memory

Only one individual, Mars, was able to pass both the training phase and the testing, correctly performing all three criteria (static, high switch and low switch), and correctly performing 14 sessions out of 15, thus with performing above 80% (i.e., 93.34% correct) in the 15 days of testing. The two females, Neptune and Callisto (females, 9 years of age) who were able to pass the training criteria, correctly performing all three criteria (static, high switch and low switch), did not pass the test criteria, with an overall score lower than 80% (respectively, 66,67% and 60,00%). All the subjects which did not pass the training criteria, Mercury, Saturn, Andromeda and Himalia, also did not pass the testing criteria, with an overall score lower than 80%.

All the scores of the testing phase can be observed in Table 4.

Name	Number of correct sessions	Performance score*
Mars	14	93,34%
Mercury	10	66,67%
Saturn	9	60,00%
Callisto	9	60,00%
Neptune	10	66,67%
Andromeda	9	60,00%
Himalia	8	53,34%

Table 4: Test phase results.

*Percentage of correct sessions over total number of sessions.

3.2.4 Hypothesis two: All individuals will perform better after training than before training

I first analysed the performance of the whole group by using a repeated-measures linear model using the subjects as the random factor. I compared the first 15 days of training (T1) with the last 15 days of training (T2) and with the 15 days of testing (Test). The results of the test can be observed in the Table 5.

Phase	β value	Standard error	p-value
T1	9.6011	0.8455	1.33e-09**
T2	-1.2880	1.1727	0.304
Test	0.2857	1.1691	0.814

Table 5: Linear model results.

The group of 7 individuals did not perform significantly better after training (i.e., during testing, Test) than before training (i.e., in the first 15 days of training, T1), (p value > 0.05). Giving the negative β value of -1.2880, I can infer that the group as a unit performed worse after training than before training.

Subsequently I runned 7 single paired t tests for dependent samples for each individual to observe whether there was an improvement in their performances individually. The results can be seen in the Table 6.

Individual	t value	p-value
Mars	-2.263	0.02028*
Mercury	0	0.5
Saturn	-0.43496	0.3351
Callisto	0.3351	0.3351
Neptune	0	0.5
Andromeda	0.3351	0.8644
Himalia	1	0.8329

Table 6: Individual t-test results for the improvement of individual performances

As expected, Mars did improve his performance significantly from the first 15 days of training to the testing phase ($p<0.05$).

Lastly, I also runned other 7 single paired t tests for dependent samples for each individual to observe whether their performance remained constant between the end of the training (last 15 days of training) and the test. The results can be seen in the Table 7.

Individual	t value	p-value
Mars	-0.56408	0.5816
Mercury	-0.80695	0.4332
Saturn	0.43496	0.6702
Callisto	-0.80695	0.4332
Neptune	-0.3669	0.7192
Andromeda	-1.1456	0.2711
Himalia	-1.1456	0.2711

Table 7: Individual t-test for the constancy of performance between end of training and testing.

All individuals did not significantly improve or worsen their performance between the last 15 days of training and the 15 days of testing ($p > 0.05$).

The graphs representing the singular performances of each individual including their relative scores during the first 15 days of training (Start), the last 15 days of training (End) and the 15 days of testing (Test) can be seen in the next page (Figure 7).

Figure 7: Individual's performance graphs.

4. DISCUSSION

4.1 DISCUSSION OF THE RESULTS

4.1.1 Hypothesis one: The blue-headed macaw, *Primolius couloni*, will be able to solve the what-where-when task using episodic-like memory.

Only one individual, Mars (male, 9 years old) was able to pass both the training phase and the testing phase, correctly performing all three criteria (static, high switch and low switch) and correctly performing 14 sessions out of 15, above 80% (i.e., 93.34% correct) in the 15 days of testing, therefore displaying episodic-like recall in a "what-where-when" memory task.

The two females, Neptune and Callisto (females, 9 years old) who were able to pass the training criteria, correctly performing all three criteria (static, high switch and low switch), did not pass the test criterion. Since between the training phase and the testing phase, there was an interchange of experimenters, the sudden change of performance of these two female subjects could have been determined by this sudden change which could have destabilize them and therefore worsen their performance. Lastly, as expected, all the subjects which did not pass the training criteria also did not pass the test.

I concluded that because one of our subjects passed the criteria for the "what-where-when" paradigm, the blue-headed macaw (*Primolius couloni*) could present elements of episodic-like memory. The social and ecological challenges that this species faces in the wild, could have favoured the evolution of the ability to recall information of particular episodes of their past in order to use it to make predictions for the future.

After the pioneering work of Clayton and Dickinson (1998) on western scrub jays (*Aphelocoma coerulescens*) it has been argued that episodic-like memory could have evolved because of their foraging strategy, driven by the necessity to remember specific food-caching episodes, therefore recalling where and when they cached different foods. Yet, among many other species, the blue-headed macaw (*Primolius couloni*) does not rely on a food-caching foraging strategy like western scrub-jays do, providing yet another proof that food-caching is not an essential feature for the evolution of episodic-like memory in non-human animals.

Babb et. al., (2006), showed how rats could episodically recall information on when and where different flavoured pallets (what) were available in a radial maze, learning that grape- and raspberry-flavoured pellets were replenished after a longer delay but not after a short delay, while chow-flavoured pellets were never replenished but were always present in the maze's rays which were not accessible earlier in the morning. Martin-Ordas et. al., (2010), showed how chimpanzees, orangutans and bonobos, also displayed episodic-like memory, being able to remember that after a short delay their preferred reward, frozen juice, was still palatable but after a long delay it would melt and not be replenished, while less-preferred rewards (i.e., grapes) were always replenished both after short and longer delays.

González-Gómez et. al., (2011) assessed the ability of hummingbirds to recall the location (where), as well as nectar quality (what) and renewal rate (when) of differently rewarding flowers, being able to recall "the most profitable nectar sources and flower position and adjust their visits to nectar renewal interval". Zentall et al. (2001), showed how pigeons are able to episodically recall whether they have pecked or refrained from pecking and signal that they remember this action using an episodic-like memory strategy.

Even invertebrates such as cuttlefishes (Jozet-Alves et. al., 2013) and honeybees (Zhang et. al., 2006, Pahl et. al., 2007) have been shown to relay on episodic-like memory to solve "what-where-when" memory tasks. Jozet-Alves et. al. (2013) showed how cuttlefishes could learn a replenishing rule in which their preferred reward (i.e., a shrimp) was replenished after a long delay but not after a short delay, while their less preferred reward (i.e., a crab) was always replenished in both kind of delays. Pahl et. al. (2007), showed how honeybees were able to remember colour, shape (i.e., what), location (i.e., where) and timing (i.e., when) of different gratings which were differently rewarded in the morning and in the afternoon.

As briefly summarized above, the body of data regarding the display of episodic-like memory in animal that do not cache food, and therefore which supports that food caching is not an essential factor for development of episodic like memory, is growing and could indeed bring more insight into the evolutionary history of episodic-like memory, together with the many socio and ecological challenges which have brought many different species to evolve this memory system.

While the literature on the ecology of blue-headed macaws (*Primolius couloni*) is still quite scarce, it is known that they feed mainly on seeds, fruits and flowers, which are distributed in relatively large rain forest patches in Peru, Brazil and Bolivia (Tobias et. al., 2007). Being able to find and extract food in variable environments (Milton, 1988, Gibson 1986) such as the rain forest, has been suggested to be one important factor for the evolution of many higher cognitive skills in primates (Emery, 2005 & 2006), like episodic-like memory, and could have also critically influenced its evolution in birds such as parrots. The blue-headed macaw could have evolved the ability to episodically recall information on the location (i.e., where) and the perishability rates (i.e., when) of different food sources (i.e., what) in their natural environment, therefore, optimizing energetically its foraging strategies.

This species tends to form large flocks of up to 60 individuals and are reported to be sedentary and gregarious (Tobias et. al., 2007). By living in complex individualized social groups, the blue-headed macaw, among other gregarious parrot species, could have evolved the ability to episodically recall information about previous social interactions linked with dominance hierarchy. Being able to remember previously experienced social interactions, whether the subject was personally involved in the social interaction or not, is essential for future decisions on "whether to engage in or refrain from antagonistic behaviours with conspecifics" (Dere, 2006).

For years now, corvids such as western scrub jays have been used as models for episodic-like memory, dictating the bases for the first paradigm which has been used to detect elements of episodic-like memory in many different non-human animal species.

As previously stated in the introduction, parrots have been shown to not only have comparable cognitive abilities and forebrain size to corvids but also to face similar sociological and ecological challenges to this species. Moreover, similarly to not only corvids but also many different animal species in which episodic-like memory has been displayed (i.e., great apes, magpies, pigeons, hummingbirds, cuttlefish etc...) parrots forage on food sources that are differently distributed in time and space and possess good visual discrimination and spatial abilities, suggesting that they should be able to recall what and where they have last eaten, as well as how long ago they ate, therefore reaching the behavioural criteria for episodic-like memory for non-human animals using a “what-where-when” paradigm (Clayton, et. al., 1998).

In this project, I present the first ever evidence that a parrot species, the blue-headed macaw, displays elements of episodic-like memory recall and might also be used in the future as a model for episodic-like memory among other species.

To summarize, I suggest that due to the social and ecological challenges that this species faces in the wild, an episodic-like memory system could have evolved favouring the ability to recall and use the information of past experienced episodes to make better predictions for future challenges.

4.1.2 Hypothesis two: all subjects learned during the training phase.

In contrast to the hypothesis, only one of the 7 individuals, Mars (male, 9 years of age) had shown a statistically significant improvement from the start of the training to the testing phase (t value = -2.263; p-value = 0.02028) having a p-value lower than 0.05. All the other subjects did not significantly improve their performance after the training period, performing equally, or even worse, than before the training period (β value = -1.2880, standard error = 1.1727, p-value = 0.304).

I suggest that the two main causes of why most of the subjects did not improve their performances during the training period could be the development of side biases and the switch of experimenters throughout the duration of the experiment

4.1.2.1 Side bias preference

Many species have shown on different occasions their predisposition to develop preferences regarding colours and shapes of objects, as well as the locations of the objects during an experiment (Kim et al., 2009; Molina et al., 2019). When subjects have this kind of preferences, it can impact the test results since the animal might ignore the initial task and choose based on their biases, leading to false conclusions on their performance (Kim et al., 2009; Molina et al., 2019).

Molina et al., (2019), showed how two African grey parrots (*Psittacus erithacus*) presented a high preference for the orange string during a string-pulling task, as well as a side bias for the string which hung from the right side, while Kim et. al.'s experiment (2009), depicted that *Amazona amazonica* are predisposed to biases regarding colour, hardness, size and material of enrichment devices choosing to interact more with specific objects than others.

Throughout the entire duration of the training phase of this experiment, all seven subjects developed, on multiple occasions, a preference for a particular side on which one of the two visual cues was positioned on the table. In the training phase, the location of the two wooden squares was stationary and never moved for the whole duration of this phase. The parrots appeared to start choosing the same location (i.e., either right or left) relatively quickly, thus maturing a side bias.

One main issue related to the maturation of the side bias could have been linked to the reward system of the stimulus choice. The only case in which the parrot would not have received any reward after its choice, was during the second stage of a 1-hour delay trial, in which the location which previously corresponded to the high-value reward (i.e., a piece of a walnut) was not replenished.

Because both the location of the two rewards (i.e., right or left) and the type of delay session (i.e., 1-hour delay or 3-hour delay) were randomized and counterbalanced, by having only two options, the probability of choosing correctly by randomly selecting the same visual cue for both stages can be relatively high and by adopting a relatively low energy strategy (i.e., always choosing the same side stimulus) the subject could often receive a reward even if the choice was incorrect.

Some individuals demonstrated to be more prone to develop a side bias than others, and some individuals also needed multiple days of side bias correction because, after a 30-minute-long session, which was the maximum amount of time for an experimental session with our subjects, they still did not choose the less-preferred side more than 2 times. One particular subject (i.e., Neptune, female born in 2014) showed to have such a strong and persistent side bias, lasting almost 20 days, that I decided to move her visual cues in order to surpass her apparent mental block and therefore start over with her training period.

Further investigations into blue-headed macaw's preferences, and into parrots' in general, could be relevant for future studies.

The side bias correction trial which I described earlier in the materials and methods, often gave good results, with the subjects understanding relatively quickly that they had to switch their choices and not always choose the same stimulus.

However, it has happened many times that while apparently "correcting" one's side bias, I would create an opposite side preference. As an example, if the bird had a left-side bias, which was successfully corrected during the correction trials (i.e., the parrot chose the less preferred side visual cue for three times in a row) the subject then developed a right-side bias which they would show in the following 4 sessions (i.e., days) which the experimenter had therefore to correct again, losing more than a week of useful data.

No data regarding any side biases development, as well as any side bias corrections during an episodic-like memory test is ever been published. This could suggest that the passing criteria for many episodic-like memory experiments in which the subjects had to discriminate between two identical options, such as in Jozet-Alves's project on cuttlefishes (Jozet-Alves et. al., 2013), was not well calibrated and should have been corrected according to the predisposition of the subjects to develop any side biases.

It is also a possibility that some animals, such as parrots, could be more prone to side biases than others. Further investigations on this matter should be carried out in future studies.

It could also be compelling to see how the subject behaviour could change by adding a second part to the side bias correction trials. To counterbalance the highly encouraged side choice done during the correction, the subject could go through a series of guiding training trials similar to the pre-training phase, but with both stimuli, in which the experimenter would guide the subject to again choose both sides randomly while getting a small reward for picking both stimuli and not uniquely one of the two.

4.1.2.2 Experimenter switch

As stated above, because of the prolonged timing of the project, the first experimenter was not able to conclude the testing with all the subjects and thus the data regarding the final days of testing of the last four subjects (i.e., Neptune, Callisto, Andromeda and Himalia) was taken by a different experimenter after the introduction of a re-training phase to give a fair chance to habituate the subjects to a new person that remained the same until the end of the study. During the collection of data of an experiment, such as this one, it would be preferable to have one single experimenter/trainer who interacts with and handles the subjects.

It has been noticed by many different trainers and students at the Comparative Cognition Research station of the Max Planck Institute for biological intelligence located at Loro Parque, Tenerife, how many different test animals (i.e., different species of parrots, bottlenose dolphins and orcas) can indeed change their behaviours based on the type of trainer/experimenter which they are interacting with. Animals could be able to learn relatively quickly that some experimenters are more prone to “close an eye” on particular mistakes and thus learn to invest less energy into the completion of the task. Yet, no investigation or data collection has been published on the matter by any of our collaborators.

It has also been noticed how different subjects can be extremely stubborn and learn particular behaviours based on the experimenter or the location or position in which the animal is been instructed to perform the behaviour, while “not being able” to execute the same exact behaviour with either a different experimenter, or while being asked to perform the behaviour in a different location. For instance, many blue-headed macaws (*Ara glaucogularis*) at our research station, would perform particular behaviours for a motor imitation test on a particular perch, but would not perform the same behaviour when placed on a different perch. No data has been published on the matter.

I therefore suggest that it could be very beneficial to repeat the experiment maintaining the same experimenter throughout the whole duration of the project.

4.1.3 Working with non-human subjects

In order to perform a cognitive test on a human, by for example questioning the subject's memory, it is strictly sufficient to ask the relative test question directly to the subject. By doing so, the probability of them understanding the question which was communicated to them is high. In contrast, without being able to verbally instruct a non-verbal subject (i.e., an animal) to solve the task, training becomes necessary. However, making sure that the non-verbal subject (i.e., the animal) is responding directly and uniquely to the stimulus, which is involved in the test, is not as easy as it may sound, since the tendency of the majority of animals to stick to irrelevant cues (Shettleworth, 2010).

The question of whether animals actually use their cognition skills to solve particular tasks as opposed to using visual, auditory or olfactory cues is still open. It has been shown that orangutans, gorillas and chimpanzees follow human gaze (Bräuer et al., 2005) and human hand-raised chimpanzees can be more successful at finding food after a plethora of different cues like vocalizations, manipulations of objects hiding the food sources ect. (Call et al., 2000). Macaques respond to pointing gestures from humans but their performance increases significantly when the experimenter is hidden behind the curtain, only showing their arms, which suggests that their presence may distract the monkeys in the "normal object-choice pointing test" (Schmitt et al., 2014).

In the African grey parrot, it has also been shown that they do use auditory cues in a food-hiding task, in which the sound coming from a box being shaken (or the absence of sound) was used to infer that the food was, or not, hidden in that box (Schloegl, 2012). Some African grey parrots also respond correctly to pointing cues as well as to steady gaze cues (Giret et al., 2009).

In order to not give any potential gazing cues to the subjects of this experiment, during the whole duration of the training and the testing phase, the experimenter wore sunglasses. Moreover the experimenter had to stay still as much as possible without moving their arms or their body in a particular direction and had to stay silent, using only the “station” and the “go” command, in order to not give any directional or verbal cues to the subjects.

4.2 DISCUSSION ON METHODOLOGY

4.2.1 Experimental setup and protocol

4.2.1.1 Different options for the setup

In the present study, different options for the visual cues were taken into consideration. I initially thought about different kind of boxes with which the bird could have interacted with, which could have made the accessibility to the reward more or less automatic.

One of the final options which "competed" with the two wooden squares which I chose in the end, consisted in a wooden box with a drawer that opened with either a nob or a piece of rope which the bird had to pull in order to get the reward. The box also had a long string attached to the back which the experimenter could pull to retrieve the boxes from the table (Figure 8).

One main problem that I thought of was the possibility for the bird to relay on olfactory cues instead of episodic memory to solve to task, since the reward was already in the box.

In the end I opted for the simpler option (i.e., two white wooden square cut-outs with a smaller black square painted in the middle) which was also the most similar to the ones used in the experiment conducted on cuttlefishes by Jozet-Alves et. al. (2013); with the initial idea to compare the two studies, I wanted the two experiments to be as similar as possible.

It could be very interesting to repeat the experiment changing the visual cues, giving the parrots more of a challenge in order to reach the reward, while increasing the reward value (i.e., bigger portions of seeds or nuts). This change could potentially motivate the subjects to learn the replenishing rule faster; since they had to use more energy to open the box, they could learn relatively faster to not waste energy by opening randomly one of the two boxes and thus following a specific rule.

The "olfactory cue" problem could be solved by building a "double base" in which to hide other types of foods which they would usually get as enrichment (such as chilli peppers and rose buds), thus covering the smell of the two distinct rewards.

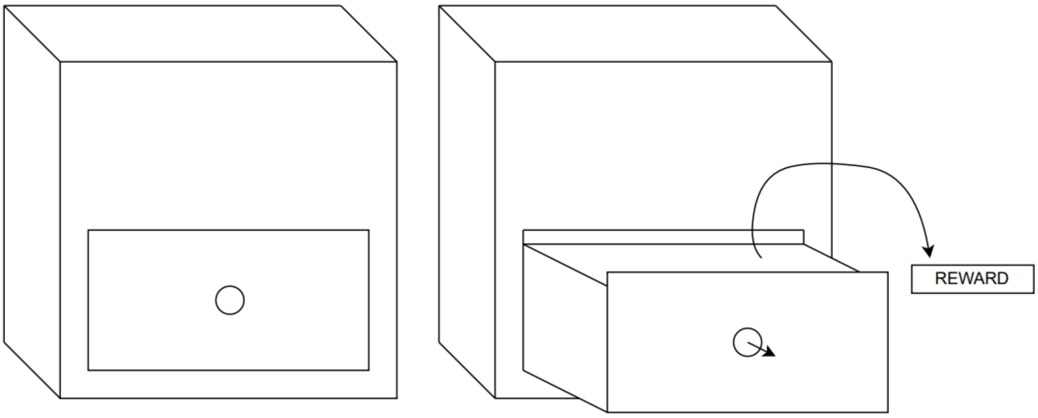

Figure 7: Original project of the visual cue.

4.2.2 Automaticity of the experiment

A minor problem which I encountered during the running of the experiment was the latency with which the subjects gained the rewards after the visual cue choice. After the subject had chosen one of the two stimuli, the presentation of the two rewards was not quite instant. Even if the experimenter was to be extremely fast, given the fact that they had to first click the clicker if the choice was correct, pick up the extendible arms and finally position them on top of the corresponding stimuli, some precious seconds would inevitably pass between the choice of the subject and the presentation of the rewards.

These few seconds occasionally permitted the bird to not come to a full stop at the stimulus which they had first chosen, and to try and touch the second stimulus in the time that it took the experimenter to present the two rewards. This led to two different scenarios which could have indeed compromise the training process: first, if the second visual cue that the subject touched would correspond to the nut (i.e., preferred reward) this could have made the subject less inclined to eat the seed, which they had chosen first but preferred less. In the second case, if the visual cue which they had chosen first was the nut, but before they had the chance to eat it, they would also touch the stimulus corresponding to the seed, the subjects could have learned that the behaviour which they just performed, that is touching both stimuli in sequence, was the correct one because it was rewarded with a big reward (i.e., a piece of nut).

A secondary minor issue that I encountered, regarded the manipulation of the separation wall. The separation wall was built to prevent the bird to reach the table, and thus to interact with the stimuli, before the experimenter had finish to setup the trial and start the recording. The problem with this curtain was that it opened from left to right (point of view of the experimenter) which could have led the bird to choose the first stimulus which they were able to see (i.e., the one of their right) instead of first look at the whole totality of the table and then choose accordingly, therefore assisting in the development of a side bias. This happened in two different occasions: first if the curtain unintentionally got stuck on the metal rod and thus stopping for a brief second, letting the bird see only one part of the table, and second in the occasion of the change of the experimenter, where the new person had yet to learn to manipulate the curtains fast enough.

It would be interesting to change the protocol so that the bird could choose, instead of two different stimuli on a table, two different locations of a touchscreen device linked to a food dispenser. This could not only help with the automatic dispensation of the reward corresponding to a particular location on the screen (i.e., choice of the subject) but could also help by decreasing the possibility that the subject could be able to touch both locations one after the other.

By using this device, the separation wall could have also been either eliminated, by teaching the bird a “wait” command, or could have been simply moved by hand, and not by strings, thus preventing it to get stuck.

4.2.3 Eliminating the human component

When conducting an experiment with an animal, it is necessary to take into consideration the human component which could have an influence on the behaviour of the subject.

During the whole duration of each session, the experimenter must not give any type of cues to the subjects, this being not moving their body into a certain direction, nor pointing to anything or giving any kind of vocal commands other than the ones needed for the experiment. The experimenter should also wear sunglasses to prevent any kind of involuntarily gazing cues by looking certain directions.

By completely, or partially, eliminating the experimenter from the room during both the training process and the test, by automating the process, the probability of giving any kind of cues to the subject would decrease to almost zero. By doing so, also any eventual changes in the experimenter, would not mutate the behaviour of the subjects.

4.2.4 Additional training

During the pre-training phase, all the subjects were trained to respond to two different commands: the "station" command, where the subject had to climb on the perch in the waiting room, and the "go" command, where the subject were encouraged to come off the perch and walk on the table to reach the stimuli.

Whether it could be possible to repeat the experiment, it could be useful to add more commands. One useful one could be a "wait" command, where the subject would learn to wait for a longer period of time on the perch, while waiting for the "go" command after the opening of the separation wall. This would give more time to bird to look at the totality of the table and to not rush over to the first stimulus they see.

A second command which could be very useful to teach to the birds, would be to come to a stop in front of the visual cue which they just touched, and thus "confirming" their choice, without moving around and touching the other one.

This kind of behaviours critically depend on the state of arousal of the subject. Whenever the animal subject gets too excited, either because of the anticipation of the food reward or for any other reason regarding the enjoyability of the test, it becomes harder for the animal to respond to the trainer's commands. This is why training, accompanied by attentiveness to the state of each individual, by always checking their weight as well as how much they eat every day or if they had any social problems with the groups (i.e., fighting), becomes essential when working with animal subjects.

The two traditional types of training used are the operant conditioning and the classical conditioning. On one hand, the classical (or Pavlovian) conditioning, also called unconscious or automatic learning, pairs an unconditional stimulus (i.e., a stimulus that leads to an automatic response), such as food, with a neutral stimulus (i.e., a stimulus which does not initially trigger any particular response), such as a particular sound or smell. By doing so, the initial neutral stimulus will be associated with the unconditional stimulus.

The operant conditioning, on the other hand, is a method of learning which uses rewards and punishments to shape a behaviour. If the behaviour is rewarded, this is most likely to reoccur and to subsequently be fixed. If the behaviour is punished, then is less likely to reoccur in the future.

4.2.5 Distractions

One final thing that should be also taken into consideration in this project is the noise and the light distractions component.

Because of the nature of the experiment, I decided to build an experimental room inside of the aviary in which the 7 subjects were housed and not in the test rooms in which all the other subjects have always been tested. As shown in Figure 4 in the materials and methods, part of this aviary was located on the outside, which was available for the visitors to see. Unfortunately, many of these visitors, as well as the tour guides, often interrupted the experimental sessions making loud noises and frightening the parrots, which resulted in the subjects getting distracted. These distractions could have indeed altered the results of the experiment.

Furthermore, as a consequence of the location of the experimental room, when one of the subjects was being trained or tested, the other 6 individuals were outside of the room often making alert calls or fighting with each other, which consequently alerted the bird which was inside, which then got distracted and often flew away from the experimental setup.

A further distraction component which should have been better taken care of, is the turning on and off of the lights in the laboratory which overlooked to the aviary. Veterinaries, zookeepers and cleaners often turned on and off the lights distracting the parrots and often frightening them.

It would be a very valuable change to move the experimental setup in a soundproof room, separated from the other individuals, with a constant lighting system and thus with fewer distractions.

5. CONCLUSIONS

I conclude that the blue-headed macaw (*Primolius couloni*) could in fact present elements of episodic-like memory given that one of our subjects passed the criteria for the "what-where-when" paradigm. The social and ecological challenges that this species faces in the wild, could have brought to the evolution of the ability to recall information of particular episodes of their part in order to use it to make predictions for the future. This study presents the first evidence of episodic-like memory in a parrot species.

I came to the conclusions that minors changes in the experimental protocol together with maintaining only one experimenter per subjects' group, might result in the display of episodic-like recall by more subjects during the full length of the experiment. Furthermore, additional investigation on parrots' inclination to side biases as well as on general information about their complex social structures and food strategies could be essential for the betterment of the future protocol.

REFERENCES

Allen, T. A., & Fortin, N. J. (2013). The evolution of episodic memory. Proceedings of the National Academy of Sciences, 110(supplement_2), 10379-10386.

Babb, S. J., & Crystal, J. D. (2006). Episodic-like memory in the rat. Current biology, 16(13), 1317-1321.

Bingman, V. P., Gagliardo, A., Hough, G. E., Ioalé, P., Kahn, M. C., & Siegel, J. J. (2005). The avian hippocampus, homing in pigeons and the memory representation of large-scale space. Integrative and Comparative Biology, 45(3), 555-564.

Bräuer, J., Call, J., & Tomasello, M. (2005). All great ape species follow gaze to distant locations and around barriers. Journal of Comparative Psychology, 119(2), 145.

Clayton, N. S., & Dickinson, A. (1998). Episodic-like memory during cache recovery by scrub jays. Nature, 395(6699), 272-274.

Clayton, N. S., Bussey, T. J., & Dickinson, A. (2003). Can animals recall the past and plan for the future?. Nature Reviews Neuroscience, 4(8), 685-691.

Clayton, N. S., Griffiths, D. P., Emery, N. J., & Dickinson, A. (2001). Elements of episodic–like memory in animals. Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences, 356(1413), 1483-1491.

Clayton, N. S., & Emery, N. J. (2015). Avian models for human cognitive neuroscience: a proposal. Neuron, 86(6), 1330-1342.

Colombo, M., & Broadbent, N. (2000). Is the avian hippocampus a functional homologue of the mammalian hippocampus?. Neuroscience & Biobehavioral Reviews, 24(4), 465-484.

Conway, Martin A. "Episodic memories." Neuropsychologia 47.11 (2009): 2305-2313.

Crystal, J. D. (2009). Elements of episodic-like memory in animal models. Behavioural processes, 80(3), 269-277.

Davidson PS, Drouin H, Kwan D, Moscovitch M, Rosenbaum RS (2012) Memory as social glue: Close interpersonal relationships in amnesic patients. Front Psychol 3:531.

Davies, J. R., Garcia-Pelegrin, E., Baciadonna, L., Pilenga, C., Favaro, L., & Clayton, N. S. (2022). Episodic-like memory in common bottlenose dolphins. Current Biology, 32(15), 3436-3442.

Day, M., Langston, R., & Morris, R. G. (2003). Glutamate-receptor-mediated encoding and retrieval of paired-associate learning. Nature, 424(6945), 205-209.

Dere, E., Huston, J. P., & Silva, M. A. D. S. (2005). Episodic-like memory in mice: simultaneous assessment of object, place and temporal order memory. Brain research protocols, 16(1-3), 10-19.

Dere, E., Huston, J. P., & Silva, M. A. D. S. (2005). Integrated memory for objects, places, and temporal order: evidence for episodic-like memory in mice. Neurobiology of learning and memory, 84(3), 214-221.

Dere, E., Silva, M. D. S., & Huston, J. P. (2004). Higher order memories for objects encountered in different spatio-temporal contexts in mice: evidence for episodic memory. Reviews in the Neurosciences, 15(4), 231-240.

Dickerson, B. C., & Eichenbaum, H. (2010). The episodic memory system: neurocircuitry and disorders. Neuropsychopharmacology, 35(1), 86-104.

Dunbar, R. I. (1998). The social brain hypothesis. Evolutionary Anthropology: Issues, News, and Reviews: Issues, News, and Reviews, 6(5), 178-190.

Eacott, M. J., Easton, A., & Zinkivskay, A. (2005). Recollection in an episodic-like memory task in the rat. Learning & memory, 12(3), 221-223.

Eichenbaum, H., & Fortin, N. (2003). Episodic memory and the hippocampus: It's about time. Current directions in psychological science, 12(2), 53-57.

Emery, N. J., & Clayton, N. S. (2004). Comparing the complex cognition of birds and primates. Comparative vertebrate cognition: are primates superior to non-primates?, 3-55.

Emery, N. J., & Clayton, N. S. (2005). Evolution of the avian brain and intelligence. Current Biology, 15(23), R946-R950.

Emery, N. J. (2006). Cognitive ornithology: the evolution of avian intelligence. Philosophical Transactions of the Royal Society B: Biological Sciences, 361(1465), 23-43.

Feeney, M. C., Roberts, W. A., & Sherry, D. F. (2009). Memory for what, where, and when in the black-capped chickadee (Poecile atricapillus). Animal cognition, 12, 767-777.

Ferkin MH, Combs A, delBarco-Trillo J, Pierce AA, Franklin S (2008) Meadow voles, Microtus pennsylvanicus, have the capacity to recall the “what”, “where”, and “when” of a single past event. Anim Cogn 11(1):147–159.

Friedman, W. J. (1993). Memory for the time of past events. Psychological bulletin, 113(1), 44.

Fugazza, C., Pogány, Á., & Miklósi, Á. (2016). Recall of others’ actions after incidental encoding reveals episodic-like memory in dogs. Current Biology, 26(23), 3209-3213.

Fugazza, C., Pongrácz, P., Pogány, Á., Lenkei, R., & Miklósi, Á. (2020). Mental representation and episodic-like memory of own actions in dogs. Scientific reports, 10(1), 1-8.

Gaffan, D. (1994). Scene-specific memory for objects: a model of episodic memory impairment in monkeys with fornix transection. Journal of Cognitive Neuroscience, 6(4), 305-320.

Gibson, K. R. (1986). Cognition, brain size, and the extraction of embedded food resources. Primate ontogeny, cognition, and social behavior.

Gilbert, P. E., & Kesner, R. P. (2002). Role of rodent hippocampus in paired-associate learning involving associations between a stimulus and a spatial location. Behavioral neuroscience, 116(1), 63.

Gilbert, P. E., & Kesner, R. P. (2003). Localization of function within the dorsal hippocampus: the role of the CA3 subregion in paired-associate learning. Behavioral neuroscience, 117(6), 1385.

Gillund, Gary. “Episodic memory” Encyclopedia of Human Behavior (Second Edition), Academic Press, (2012) , 68-72

Giret, N., Miklósi, Á., Kreutzer, M., & Bovet, D. (2009). Use of experimenter-given cues by African gray parrots (Psittacus erithacus). Animal Cognition, 12, 1-10.

González-Gómez, P. L., Bozinovic, F., & Vásquez, R. A. (2011). Elements of episodic-like memory in free-living hummingbirds, energetic consequences. Animal Behaviour, 81(6), 1257-1262.

Griffiths, D., Dickinson, A., and Clayton, N. (1999). Episodic memory: what can animals remember about their past? Trends Cognit. Sci. 3, 74–80.

Hassabis, Demis, and Eleanor A. Maguire. "Deconstructing episodic memory with construction." Trends in cognitive sciences 11.7 (2007): 299-306.

Holland, S. M., & Smulders, T. V. (2011). Do humans use episodic memory to solve a What-Where-When memory task?. Animal cognition, 14(1), 95-102.

Humphrey, N. K. (1976). The social function of intellect. Growing points in ethology, 37(1), 303-317.

Jozet-Alves, C., Bertin, M., & Clayton, N. S. (2013). Evidence of episodic-like memory in cuttlefish. Current Biology, 23(23), R1033-R1035.

Ksepka, D. T., Balanoff, A. M., Smith, N. A., Bever, G. S., Bhullar, B. A. S., Bourdon, E., ... & Smaers, J. B. (2020). Tempo and pattern of avian brain size evolution. Current Biology, 30(11), 2026-2036.

Lo, K. H., & Roberts, W. A. (2019). Dogs (Canis familiaris) use odor cues to show episodic-like memory for what, where, and when. Journal of Comparative Psychology, 133(4), 428.

Martin-Ordas, G., Haun, D., Colmenares, F., & Call, J. (2010). Keeping track of time: evidence for episodic-like memory in great apes. Animal cognition, 13, 331-340.

McRae, Ken, and Michael Jones. 14 Semantic Memory. Vol. 206. Oxford: Oxford University Press, 2013.

Milton, K. (1988). Foraging behaviour and the evolution of primate intelligence.

Nomura, T., & Izawa, E. I. (2017). Avian brains: Insights from development, behaviors and evolution. Development, growth & differentiation, 59(4), 244-257.

Olkowicz, S., Kocourek, M., Lučan, R. K., Porteš, M., Fitch, W. T., Herculano-Houzel, S., & Němec, P. (2016). Birds have primate-like numbers of neurons in the forebrain. Proceedings of the National Academy of Sciences, 113(26), 7255-7260.

Pahl, M., Zhu, H., Pix, W., Tautz, J., & Zhang, S. (2007). Circadian timed episodic-like memory–a bee knows what to do when, and also where. Journal of Experimental Biology, 210(20), 3559-3567.

Panoz-Brown, D., Corbin, H. E., Dalecki, S. J., Gentry, M., Brotheridge, S., Sluka, C. M., ... & Crystal, J. D. (2016). Rats remember items in context using episodic memory. Current Biology, 26(20), 2821-2826.

Pause, B. M., Zlomuzica, A., Kinugawa, K., Mariani, J., Pietrowsky, R., & Dere, E. (2013). Perspectives on episodic-like and episodic memory. Frontiers in Behavioral Neuroscience, 7, 33.

Rajji, T., Chapman, D., Eichenbaum, H., & Greene, R. (2006). The role of CA3 hippocampal NMDA receptors in paired associate learning. Journal of Neuroscience, 26(3), 908-915.

Roberts, A. C. (1996). Comparison of cognitive function in human and non-human primates. Cognitive Brain Research, 3(3-4), 319-327.

Roberts WA (2002) Are animals stuck in time?Psychol Bull128(3):473–489

Saumier, Daniel, and Howard Chertkow. "Semantic memory." Current neurology and neuroscience reports 2.6 (2002): 516-522.

Sherry, D. F. (2006). Neuroecology. Annu. Rev. Psychol., 57, 167-197.

Schmitt, V., Schloegl, C., & Fischer, J. (2014). Seeing the experimenter influences the response to pointing cues in long-tailed macaques. PloS one, 9(3), e91348.

Schnell, A. K., Clayton, N. S., Hanlon, R. T., & Jozet-Alves, C. (2021). Episodic-like memory is preserved with age in cuttlefish. Proceedings of the Royal Society B, 288(1957), 20211052.

Schloegl, C., Schmidt, J., Boeckle, M., Weiß, B. M., & Kotrschal, K. (2012). Grey parrots use inferential reasoning based on acoustic cues alone. Proceedings of the Royal Society B: Biological Sciences, 279(1745), 4135-4142.

Schwartz, B. L., & Evans, S. (2001). Episodic memory in primates. American Journal of Primatology: Official Journal of the American Society of Primatologists, 55(2), 71-85.

Schwartz, B. L., Colon, M. R., Sanchez, I. C., Rodriguez, I., & Evans, S. (2002). Single-trial learning of" what" and" who" information in a gorilla (Gorilla gorilla gorilla): implications for episodic memory. Animal Cognition, 5(2), 85-90.

Singer, R. A., & Zentall, T. R. (2007). Pigeons learn to answer the question “where did you just peck?” and can report peck location when unexpectedly asked. Learning & Behavior, 35(3), 184-189.

Squire, Larry R. "Declarative and nondeclarative memory: Multiple brain systems supporting learning and memory." Journal of cognitive neuroscience 4.3 (1992): 232-243.

Striedter, G. F. (2005). Principles of brain evolution. Sinauer associates.

Suddendorf, T., & Corballis, M. C. (2010). Behavioural evidence for mental time travel in nonhuman animals. Behavioural brain research, 215(2), 292-298.

Suddendorf, T., Addis, D. R., & Corballis, M. C. (2009). Mental time travel and the shaping of the human mind. Philosophical Transactions of the Royal Society B: Biological Sciences, 364(1521), 1317-1324.

Tobias, J. A., & Brightsmith, D. J. (2007). Distribution, ecology and conservation status of the Blue-headed Macaw Primolius couloni. Biological Conservation, 139(1-2), 126-138.

Torres Ortiz, S., Smeele, S. Q., Champenois, J., & von Bayern, A. M. (2022). Memory for own actions in parrots. Scientific Reports, 12(1), 20561.

Tulving, E. "Precis of elements of episodic memory." Behavioral and Brain Sciences 7.2 (1984): 223-238.

Tulving, E., and Markowitsch, H.J. (1998). Episodic and declarative memory: role of the hippocampus. Hippocampus 8, 198–204.).

Tulving, Endel. "Episodic and semantic memory." (1972).

Tulving, Endel. "Episodic memory: From mind to brain." Annual review of psychology 53.1 (2002): 1-25.

Ullman, Michael T. "Contributions of memory circuits to language: The declarative/procedural model." Cognition 92.1-2 (2004): 231-270.

Van Horik, J. O., Clayton, N. S., & Emery, N. J. (2012). Convergent evolution of cognition in corvids, apes and other animals.

Van Lawick-Goodall, J. (1971). Tool-using in primates and other vertebrates. In Advances in the Study of Behavior (Vol. 3, pp. 195-249). Academic Press.

Zentall, T. R., Clement, T. S., Bhatt, R. S., & Allen, J. (2001). Episodic-like memory in pigeons. Psychonomic bulletin & review, 8(4), 685-690.

Zentall, T. R., Singer, R. A., & Stagner, J. P. (2008). Episodic-like memory: pigeons can report location pecked when unexpectedly asked. Behavioural Processes, 79(2), 93-98.

Zhang, S., Schwarz, S., Pahl, M., Zhu, H., & Tautz, J. (2006). Honeybee memory: a honeybee knows what to do and when. Journal of Experimental Biology, 209(22), 4420-4428.

Zhou, W., & Crystal, J. D. (2011). Validation of a rodent model of episodic memory. Animal cognition, 14, 325-340.

Zhou, W., Hohmann, A. G., & Crystal, J. D. (2012). Rats answer an unexpected question after incidental encoding. Current biology, 22(12), 1149-1153.

Zinkivskay, A., Nazir, F., & Smulders, T. V. (2009). What–where–when memory in magpies (Pica pica). Animal cognition, 12, 119-125.

1. APPENDIX

1.1 A word on the success criterion

I first decided to run this project after an experiment conducted by Jozet-Alves et. al. (2013) on episodic-like memory in cuttlefishes caught my attention. In this experiment Jozet-Alves and colleagues proposed that because of their foraging behaviour as well as their good visual discrimination and spatial abilities, cuttlefishes could be able to recall what and where they have last eaten, as well as how long ago they ate, therefore reaching the behavioural criteria for episodic-like memory for non-human animals using a “what-where-when” paradigm (Clayton, et. al., 1998, Jozet-Alves et. al. 2013).

I initially decided to base our experimental protocol on this project’s by using a similar setup as well as the same passing criteria for the training and testing phases (8 correct sessions out of 10 consecutive sessions) with the initial idea to compare the two. Within the first 11 days of training, 3 subjects had already passed the criteria (Himalia, 10 days, Neptune, 10 days and Mars, 11 days) similarly to the three cuttlefishes studied by Jozet-Alves et. al. (2013) (2 cuttlefishes reached the criteria in 10 days and the third one reached it in 12). Other 3 subjects reached the criteria within 25 days (Mercury, 15 days, Callisto, 20 days and Andromeda 25 days). Only one subject, Saturn, did not reach the criteria during the whole duration of the training phase, performing at most 7 correct sessions out of 10 consecutive sessions.

Within the first 10 days of training, I started to notice how some of them were always choosing the same side while others preferred to always switch between the first and the second stage, choosing therefore a “strategy” to resolve the problem present to them. I also took into consideration that it could be very unlikely that many individuals had picked up the replenishing time rule in such a short amount of time. With this I decided to extend the period of the training phase when, eventually, all the individuals started to either choose the stimuli completely randomly or to always stick to one location (i.e., side bias), while also changing their behavioural strategies from time to time.

I concluded that the initial criterion was not well suited for our subjects' group, and I therefore decided to modify the passing criterion making it more stringent.

I introduced 3 types of sessions: a static session in which the subject chose the same side for both stages, and two types of switch sessions, in which the subject switched its choice between the two stages, a high switch session (i.e., from nut to seed) and a low switch session (i.e., from seed to nut), Table 1.

Sessions	**Definition**	**Types**
Static session	The subject chooses the same side for both stages	1h-delay: seed-seed
		3h-delay: nut-nut
Switched session	The subject switches their choice between the two stages	**High switch**, 1h-delay: nut-seed
		Low switch, 3h-delay: seed-nut

Table 1: Types of sessions.

After establishing the different types of sessions, we decided that in order to pass to the testing phase, each subject had to make 8 correct high switches in 10 consecutive high switched sessions, 8 correct low switches in 10 consecutive low switched sessions, as well as 8 correct static sessions in 10 consecutive static sessions. If the subjects reached the new criteria, they could go through the testing phase.

We also added that if the subjects did not reach the criteria within 90 overall sessions, we considered them to have not learn the rule and would therefore pass to the testing phase to observe whether they would stay consistent and not pass the test or if daily changing the location of the stimuli would change the results.

For the testing we decided to test the birds over a period of 15 days, keeping the passing criterion to an 80% overall correct score.

In absence of any data regarding any particular side bias preference in the cuttlefish experiment conducted by Jozet-Alves et. al. (2013), as well as in any other paper which showcases episodic-like memory in many mammals and bird species, I argue that the cuttlefishes, and possibly other species, may have been able to pass the training criteria, not by fully understanding the concept and the replenishing time rule of the "what-where-when" paradigm but by performing either randomly or by having a strong side biases which were not taken into account.

1.2 A word on the food-preference test

I tried multiple combinations of seeds (sunflower and pumpkin seeds), nuts (walnuts and pecan nuts) and fruits (bananas and grapes), and after 13 days of testing, the best combination of rewards was walnut, as the preferred reward, being chosen 9 times out of 10 for 2 days in a row, and sunflower seed, as the least preferred reward, being chosen 1 time out of 10 for 2 days in a row.

I carried out multiple combination of food rewards in the food-preference test in order to find the best combination with each individual showing a clear preference for one of the two rewards while still showing that they could eat the less-preferred reward in case of a 1-hour trial in which the preferred reward was not replenished after the delay. We also decided that we wanted to keep the same two rewards for all individuals to have a group as homogeneous as possible.

No individual showed a particular preference for fruits like grapes and bananas when compared with nuts (either macadamia nuts or walnuts) or with seeds. No individual showed a particular preference for either of the two nut proposals when compared to each other. Some individuals showed a preference for pumpkin seeds when compared to walnuts and macadamia nuts but this preference did not show in all individuals.