Memory in dolphins and parrots: a comparative perspective

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II. **S. Torres Ortiz**, S. Q. Smeele, J. Champenois, A. M. P. von Bayern. (submitted: Scientific Reports). What did I do? Memory for own actions in parrots. https://dx.doi.org/10.21203/rs.3.rs-2098690/v1
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III. **S. Torres Ortiz**, S. Q. Smeele, C. Ubero Ramírez, A. M. P. von Bayern. (in prep). Memory for actions in parrots, dolphins, and pinnipeds: a comparative approach

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I. **S. Torres Ortiz**, A. Corregidor Castro, T. J. S. Balsby, and O. N. Larsen. (2020). Problem-solving in a cooperative task in peach-fronted conures (*Eupsittula aurea*). Animal Cognition, 23(2), 265-275.

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Author contribution

- Summary, General Introduction, and Discussion - Written by Sara Torres Ortiz. Summary Translation: Andreas Fackel.

- Study 1 – Dolphins memorize what to do for the future and what they did in the past episodically – Auguste von Bayern and Sara Torres Ortiz conceived the idea of the experiment. Sara Torres Ortiz, Andrea Martin Guerrero, and Cristina Ubero Ramírez performed the experiments. Simeon Quirinus Smeele and Sara Torres Ortiz analysed and interpreted the results. Sara Torres Ortiz wrote the manuscript with feedback from Auguste von Bayern and Simeon Quirinus Smeele.
- Study 2 – What did I do? Memory for own actions in parrots – Sara Torres Ortiz conceived the idea which was developed with Auguste von Bayern. Sara Torres Ortiz and Juliette Champenois performed the experiments. Simeon Quirinus Smeele and Sara Torres Ortiz analysed and interpreted the results. Sara Torres Ortiz wrote the manuscript with feedback from Auguste von Bayern and Simeon Quirinus Smeele.
- Study 3 – Memory for actions in parrots, dolphins, and pinnipeds: a comparative approach – Sara Torres Ortiz and Simeon Quirinus Smeele conceived the idea of the experiment, and it was developed with Auguste von Bayern. Sara Torres Ortiz and Cristina Ubero performed the experiments. Simeon Quirinus Smeele and Sara Torres Ortiz analysed and interpreted the results. Sara Torres Ortiz wrote the manuscript with feedback from Auguste von Bayern and Simeon Quirinus Smeele.

Summary

Human memory has interested writers and philosophers since ancient times. However, it is psychologists who first tried to understand the functioning of memory. Memory is essential for humans, without it, we could not function in the present and plan for the future. We would also not be able to learn anything. Humans and animals modify their behaviour as a consequence of learning. Thanks to memory processes, the information learned is constantly updated and retained in the brain.

This thesis aims to investigate the yet hardly studied memory of two distantly related species: parrots and dolphins. In three studies, I investigated the existence of short-term and long-term episodic-like memory for self-performed actions in both species.

In the first study, I investigated the existence of prospective and episodic-like memory in dolphins. We instructed five trained bottlenose dolphins to memorize specific arbitrary self-performed actions, which they, upon later request with a specific hand command, should reiterate. All dolphins remembered a single action after 16 hours. To better understand if the encoding was semantic or episodic, two control dolphins that had not experienced need in the distant future (never having experienced delays exceeding 3 min) were tested in an unexpected recall test 2 hours and 16-17 hours later. They could successfully recall the action they were supposed to display suggesting a episodic-like memory system at work. Two of the five delay experienced test dolphins recalled arbitrary sequences of two actions after two hours and three actions after 15 minutes. One of them was also trained to reverse the order of the action sequence to investigate whether it encoded a fixed order or ordered elements. It could spontaneously reverse 2 remembered actions. Lastly, we tested the control dolphins in a condition where the action was not self-performed after 10 seconds (in a short-term memory condition) and 60

seconds (in a long-term memory condition). In this condition, the experimenter instructed the dolphins which action to memorize but without letting the dolphin self-perform it until the respective delay finalized. Our last experiment showed that the dolphins were remembering their own-actions as they could remember the experimenter command after 10 seconds but not after a longer delay of 60 seconds.

In the second study, I investigated whether blue-throated macaws, a social parrot species, could remember their previous self-performed actions. The parrots were trained to repeat four learned actions upon command employing the “repeat paradigm”, developed by Mercado et al. 1998 on dolphins. Test sessions included repeat trials, double repeat trials, intermixed with trials without repeat. These sessions tested if the parrots repeated correctly only when requested and not relying on a representation of the last behavioural command. All parrots were able to perform single and double repeats well above chance level. To better understand their memory abilities, the parrots also received sessions with increasing time delays preceding the repeat command. The parrots could remember their own actions for delays up to 12-15 seconds. In a final test, I examined whether the parrots had generalised the concept underlying the “repeat what you just did” command. It tested the parrots’ ability to transfer the repeat concept, to an untrained situation, i.e., to 3 newly trained behaviours, which they had never repeated before, spontaneously at the first trial, and in a second trial intermixed with the already trained actions (untrained repeat tests). The parrots were able to generalize the abstract rule of repeating right after the delay testing, therefore, after learning to repeat four actions.

In the third and last study, we employed the exact same method, i.e., the “repeat paradigm” on three dolphins. We trained them to perform the same experiment as the parrots in the second study, in order to compare their performance directly and also with the performance of three species of pinnipeds tested as part of my previously published work. We performed a metanalysis using Bayesian models to have a direct comparison of the memory performance of the five different species. The aim of this study was to better understand the cognitive evolution of memory for self-performed actions, which is regarded as a building component of self-representation and episodic-like memory, and may have evolved early in vertebrate evolution. We employed the “repeat paradigm” using identical methods comparing distantly related taxa directly. To our knowledge, with five different species of three different taxa, this study provides the largest direct comparison of memory for self-performed actions testing and reveals that all species performed very similarly in all conditions despite their evolutionary distance.

Zusammenfassung

Historisch gesehen ist das Gedächtnis seit der Antike für Schriftsteller und Philosophen von Interesse. Aber es waren Psychologen, die als Erste versucht haben, die Funktionsweise des menschlichen Gedächtnisses zu entschlüsseln. Das Gedächtnis ist für den Menschen lebensnotwendig. Menschen und Tiere verändern ihr Verhalten als Folge des Lernens. Dank der Gedächtnisprozesse werden die gelernten Informationen immer aktualisiert und im Gehirn gespeichert.

Das Ziel dieser Arbeit ist es, die bisher kaum erforschten Gedächtnisfähigkeiten zweier entfernt verwandter Arten zu untersuchen, Aras und Delfine. Ich untersuche deren episodisches Kurzzeit- und Langzeitgedächtnis für eigene Handlungen.

In der ersten Studie untersuchte ich die Existenz von prospektivem und episodischem Gedächtnis bei/von Delfinen. Für diese Studie arbeiteten wir mit fünf schon bereits trainierten Großen Tümmlern. Die Delfine sollten sich eine bestimmte, willkürlich ausgewählte, antrainierte Handlung merken und diese später auf ein Signal hin zu wiederholen. Alle Delfine erinnerten sich noch nach 16 Stunden an diese Handlung und konnten sie ausführen. Um näher zu untersuchen, ob die Gedächtnis-Codierung prospektiv oder episodisch war, wurden zusätzliche Daten von drei Delfinen als Kontrolle für dieses Experiment eingeholt. Diese Delfine waren nicht wie die anderen Delfine darauf trainiert worden, sich eine bestimmte Handlung für länger als 3 Minuten in der Zukunft zu merken. Diese Delfine wurden einem „unerwartetem Erinnerungs-Test“ nach 2 Stunden unterzogen. Alle drei erinnerten sich daran, welche Handlung sie ausführen sollten. Der Kontrolltest erbrachte daher einen Beweis dafür, dass die Delfine mit hoher Wahrscheinlichkeit kein prospektives, sondern ein retrospektives episodisches Gedächtnis-System zu nutzen schienen. Für das nächste Experiment wurden zwei der

fünf trainierten Test-Delphine ausgewählt. Die Tiere konnten sich an eine Sequenz von zwei Handlungen nach zwei Stunden und an drei Handlungen nach 15 Minuten erinnern. Einer dieser beiden Delfine wurde auch darauf trainiert, in jeder Sequenz die Reihenfolge der Handlungen umzukehren, um herauszufinden wie die Sequenzen im Gehirn des Delfins verschlüsselt sind, d.h., als eine fixe Sequenz oder in einer bestimmten Reihenfolge angeordnete Elemente. Der Test-Delfin war fähig die Reihenfolge eine Zweier-Sequenz spontan umzudrehen. Schließlich testeten wir die Kontrolldelphine in einem Zustand, in dem die Aktion nach 10 Sekunden (in einem Kurzzeitgedächtniszustand) und 60 Sekunden (in einem Langzeitgedächtniszustand) nicht selbst ausgeführt wurde. In diesem Zustand wies der Experimentator die Delfine an, welche Aktion sie sich merken sollten, ohne den Delfin sie selbst ausführen zu lassen, bis die jeweilige Verzögerung abgeschlossen war. Unser letztes Experiment zeigte, dass sich die Delfine an ihre eigenen Aktionen erinnerten, da sie sich nach 10 Sekunden an den Befehl des Experimentators erinnern konnten, aber nicht nach einer längeren Verzögerung von 60 Sekunden.

In der zweiten Studie untersuchte ich, ob Blaukehlaras, eine hochsoziale Papageienart, sich an ihre vorherigen eigenen Handlungen (vier verschiedene antrainierte Verhaltensweisen) erinnern kann und implementierten den von Mercado et al. 1998 entwickelten „Repeat Paradigm“. Dazu wurden die Papageien darauf trainiert, vier erlernte Verhaltensweisen auf einen bestimmten Befehl hin zu wiederholen. Die Testsitzungen in diesem Experiment beinhalteten Tests, bei denen eine einzelne Handlung wiederholt wurde, Tests, für die eine doppelte Wiederholung gefordert wurde und Tests in denen eine Handlung ohne Wiederholung ausgeführt werden sollte. Um zu kontrollieren, ob die Papageien nur dann wiederholten, wenn sie dazu aufgefordert wurden anstatt sich an das zuletzt gegebene Kommando zu erinnern, wurden diese

Wiederholungen in zufällig angeordneter, gemischter Reihenfolge abgefragt. Um die Gedächtnis-leistung der Papageien zu untersuchen, gab es ferner auch Testsitzungen mit zunehmender Zeitverzögerungen vor dem Wiederholungsbefehl. In dem letzten Experiment wurde getestet, ob die Papageien das dem „Wiederhol-Befehl" zugrunde liegende Konzept verstanden hatten und auf eine neue noch nicht trainierte Situation (neuerlernte, noch nie zuvor wiederholte Handlungen) zu übertragen. Die Aras waren fähig, die neuen Handlungen auf Anhieb, also beim ersten Versuch, zu wiederholen und konnten wiederholen dieselbe neue Handlung auch ein 2. Mal wiederholen, wenn sie unter das vier bekannte Verhalten gemischt abgefragt wurde.

In der dritten und letzten Studie implementierten wir den oben beschriebenen Repeat-Paradigm mit der identischen Methodik wie zuvor in der zweiten Studie mit den Blaukehlaras an drei großen Tümmlern, um einen direkten Vergleich zu erzielen. Daraufhin wurden die Ergebnisse der Delfine mit den Ergebnissen der Blaukehlaras aus der zweiten Studie und einer zuvor veröffentlichten Studie an drei Arten von Flossenfüßer verglichen. Wir haben eine Metaanalyse mit Bayesian Modellen durchgeführt, um einen direkten Vergleich der Gedächtnisleistung der fünf verschiedenen Arten zu erhalten. Das Ziel dieser Studie war es, die Natur der kognitiven Evolution und der komplexen Kognition, in diesem Fall mit einer Aufgabe zum Gedächtnis für eigene Handlungen, durch Testen und Vergleichen entfernt verwandter Taxa besser zu verstehen. Unseres Wissens nach, umfasst diese Studie mit fünf direkt miteinander verglichenen, verschiedenen Arten den größten Vergleichsdatensatz zum Gedächtnis für selbst ausgeführte Handlungen.

Introduction

1. Memory: Structure and processes

Human memory is a mental faculty by which information is encoded, stored and retrieved when required by the individual (Tulving, 1985). Thanks to memory processes and the access we have to our past experiences, we are rarely helpless in new situations. Every new situation an individual encounters, reminds it of a previous experience (Gershman & Daw, 2017). Our access to memories occurs so swiftly that we barely notice our constant dependence on memory retrieval. Memory is essential to our lives in order to operate in the present or think about the future. There is no proven limit to the amount of information that can be stored in our long-term memory (Cowan, 2008). However, we cannot remember everything that ever happened, so there must be a cost to the amount of information stored (Collins & Quillian, 1969). An economic point of view can explain the way we acquire, maintain and use our knowledge (Rescher, 1989). This chapter is primarily focussed on the definitions of different types of memory, their classification according to different criteria and major theories and description of their function.

1.1 Structural model of memory

Memory is a complex psychological and neurological process that is used to code information, store it in the brain and recover at a later moment in time. Research in amnesiac patients led to the proposed existence of different memory systems (Warrington & Weiskrantz, 1970, 1978). Patients behaved normally in memory tasks when they were not asked to retrieve memories in a voluntary manner, since they failed in conscious retrieval of memories when they were asked. Advances in this line of research, has disclosed that different brain structures are responsible for different types of memory (Squire, 2004; Tulving, 1985; Tulving & Schacter, 1990).

For humans, the most widely accepted model to explain the structure of memory was proposed by Atkinson & Shiffrin (1968) (Atkinson & Shiffrin, 1968). According to this model, memory consists of several main structures that represent different storages. Information moves between the storages through a series of control processes. In this model, the three storages are sensory memory, short-term memory and long-term memory (Figure 1).

According to Atkinson & Shiffrin's model, information from the environment arrives to the sensory memory, and from there, information transfers to the short-term memory. This information decays rapidly. An important function of the short-term memory storage is choosing which information should get transferred to the long-term memory. The long-term memory is a permanent or almost permanent memory system storage. According to Broadbent (2013), the selective filter for information between the sensory store and the short-term memory was attention: Only the attentional information could become conscious information and therefore, be stored in the short-term memory and subsequently the long-term memory.

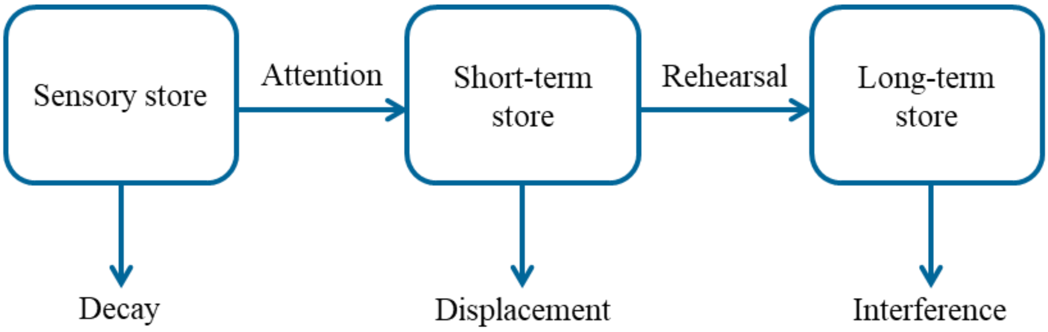


Figure 1. *The multi-storage model explaining the information flow between different memory systems. From: Cognitive psychology: a student's handbook* (Eysenck & Keane, 2015).

The multi-storage model has several strengths but also limitations. The distinction between the three memory stores make sense as they differ in several aspects:

- Temporal duration
- Storage capacity
- Oblivion mechanism
- Effects of brain damage

The multi-storage model, however, has four main limitations:

- The model assumes that short- and long-term memory are independent units and operates in a single uniform way. More recent models divide short- and long-term memory into more subunits or components (Van Houdt et al., 2020).
- This model is assuming that the information needs to first pass by the short-term memory storage before it can go into the long-term store. However, behavioural experiments have shown that the information processed in short-term memory has already made contact with information stored in the long-term memory.
- It is assumed that short-term memory only stores conscious information. On the other hand, implicit memory, where recollection of past events occurs unconsciously and unconscious learning has already been proven to exist.
- The model assumes that the majority of information gets transferred into long-term storage through rehearsal. The role of rehearsal in human daily life is however very limited, suggesting that other mechanisms also help transferring memories from short- to long-term storage.

2. Sensory memory

The sensory information arrives through different senses (visual, auditory, tactile, gustatory, olfactory, etc) and remains in the sensory register usually less than one second. Afterwards, sensory information decays and is lost. If information is processed by the cognitive system and moves to the short-term memory (Eysenck & Keane, 2015).

Sensory memory is related to perception, and its characteristics are very different, depending on the sensory modality (Table 1). Each modality has its own sensory storage, but the most studied ones are visual and auditory senses. The visual sensory memory can hold information for about one second, according to Sperling (1963). This type of memory is also referred to as iconic memory and appears to be particularly visual in character. The auditory sensory memory can hold information briefly, according to some experiments up to 10 seconds. This type of memory is also be called echoic memory.

If the information arriving from the environment to the sensory systems is not attended quickly, this information is then lost.

3. Short-term memory

Short-term memory preserves a small quantity of information for a short period of time (Tulving, 1985). If the information arriving to the sensory memory is attended, then, before going into a relatively permanent long-term memory, this information will go into an intermediate short-term memory, where it can be rehearsed. Short-term memory and working memory are two different theoretical concepts that sometimes are not strictly separated in the literature (Aben et al., 2012). Short-term memory refers to the maintenance of the information, and working memory refers to maintenance plus manipulation (Cowan, 2008). The distinction between short-term memory and working memory is still unclear from an experimental point of view; behavioural and neuroimaging studies cannot find clear distinctions between the two types of memory (Aben et al., 2012).

For humans, the number of independent elements that can be stored in this type of memory are between five and nine, with a mean of seven elements. The maximum duration between remembering and recalling is from 10 to 30 seconds (Baddeley & Warrington, 1970). Short-term memory also has important control functions regarding the type of information that it receives. Those functions range from repetition and codification of the information received, as well as the decision to store the data into the long-term memory system. This memory system is highly affected by distractions, resulting in the individual forgetting information to be remembered.

Regarding the retrieval system for short term memory, Sternberg (S. Sternberg, 1969, 1975) suggested that the retrieval from short-term memory is different from long-term memory. The author suggested that while the retrieval process in short-term memory is serial referred to the act of attending to and processing one item at a time, the retrieval from long-term memory is in parallel while parallel where the act of attending to and processing all items is simultaneous.

4. Long-term memory

Long-term memory stores significant facts permanently, or almost permanently. It includes information about personal experiences, but also on data, facts and events that are not personally experienced (Table 1).

Nowadays, long-term memory is divided into two different types: explicit or declarative memory and implicit or non-declarative memory associated with different parts of the brain (Clark, 2017; Figure 2). Information from declarative memory can voluntarily be retrieved in a conscious manner. Declarative memory refers to memories that can be described. In contrast, non-declarative memory is not affected by repetition and distractions, and it does not require the medial temporal lobe in the brain, which is the brain structure needed for conscious memory (Daselaar et al., 2006). This memory does not involve conscious recollection. It is a type of memory that influences behaviour and is related with the ability of knowing how to do certain things, like driving a car or how to walk.

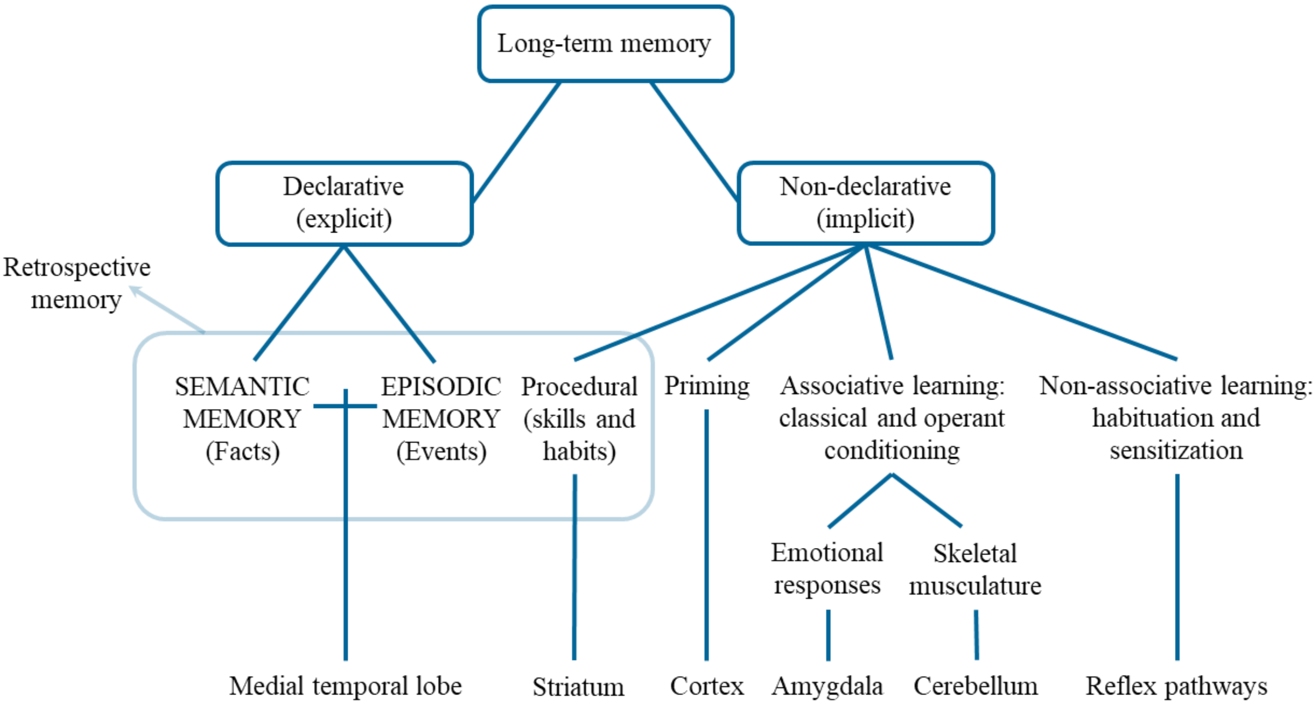


Figure 2. *Main forms of long-term memory and their associated brain structures. From: (Kandel et al., 2000).*

Evidence of several long-term memory systems comes mainly from brain damaged human patients. Patients with amnesia have great difficulties in forming declarative memories, but their ability to form non-declarative memories is barely intact.

In declarative memory, the memory of personally experienced events is named “episodic memory” whereas the memory of general knowledge, facts, word meaning and people is called “semantic memory”.

For non-declarative memory, (Schacter & Slotnick, 2004) identified two systems: the perceptual representation system, which operate perceptual information about the form and structure of objects and words, and the procedural memory, which refers to learning of cognitive and motor skills. But referring back to Figure 2, there are other forms of non-declarative memory as habituation, sensitization, classical and operant conditioning.

4.1. Semantic memory

Semantic memory is an extensive memory consisting of knowledge of lexicon, concepts and categories. Concepts and categories are mental representations organizing the different objects in the world in classes. Without them, we would need to store each element, object or event in a different place with each own “name” to distinguished each other, therefore, concepts and categories represent great cognitive savings (Rosch & Lloyd, 1978). Semantic memory is a type of declarative and conscious memory needed for general knowledge and language. These memories are not linked to a particular temporal or spatial context. Therefore, it refers to the meaning, comprehension and other generalized concepts that are not related to specific experiences or events. Semantic memory makes the acquisition and retention of information about the world possible, in a broad and general sense.

Inside the semantic memory, there is a great diversity of concepts that are very well organized. The speed of the knowledge retrieval from the semantic storage is possible because of the perfect organization of the concepts (Eysenck & Keane, 2015).

Concepts are the main units of human thinking and are considered by psychologists as mental representations. Even though concepts are not equivalent to the words that represent them, there is a close relationship between them. Categories are the representations of specific exemplars of existing concepts in memory and are the main elements of thinking that make cognitive economy possible (Barsalou, 1992; Margolis, 1994). If concepts did not exist, we would need to store each individual entity, object or event by its name in order to distinguish it from the rest, which could overload the memory system (Eysenck & Keane, 2015).

4.2. Episodic memory

Episodic memory is a declarative long-term memory, that allows voluntary recalls of specific experiences of the individual and what happened in a specific temporal situation (Table 1). Tulving (Tulving, 1985) defined episodic memory as “the memory for personally experienced events”, so it is related to the autobiographic events in a persons’ life. The retrieval from this memory store occurs voluntarily and in a conscious manner. The person needs to travel back in time with their mind to the event that wants to be recalled in order to be able to access that memory content. Episodic memory depends on the capacity to codify and recover specific events at a specific moment. The properties that distinguish episodic memory are:

1) The existence of a temporal factor; every fact or event that we try to recall from episodic memory has a very specific temporal moment.

2) Spatial and perceptive information; the person will remember both where the particular event took place and also, the shapes, colours, sounds and smells that accompanied that event.

3) The experience of the event in first person; the person feels that he or she was the main character of the event that he or she is trying to recall.

4) Conscious access to the memory contents; there are four modalities encoding episodic memory: Acoustical, visual, semantic, and motor actions.

Episodic memory develops late during childhood and reaches highest performance in adults (Shing & Lindenberger, 2011). During senescence, it deteriorates slowly in humans and other mammal species like dogs (Sanches et al., 2022) but seems to be preserve in other species, like cuttlefish (Schnell et al., 2021). This memory system is oriented towards the past and is more vulnerable to neurological deterioration than other types of memory (Cansino, 2009). It allows the individual to mentally travel back in time to events that happened in the past.

The ability to recover information from episodic memory is closely related to the meaning of the memories and how those memories are organized. Effective methods organizing the material stored from episodic memory are the hierarchical organization and the establishment of relationships between concepts, to build a storyline (Anderson, 2005).

The time dedicated to actively encode the information will have an effect in the later recall of memories. The more time the subject is dedicated to process information, the better the information will be remembered. When the information is presented in an organized manner, the subject can remember it more easily. Thus, when we want to retain material in our mind, we try to impose a subjective organization of the information in order to process it and remember it better. For example, it has been observed that people will repeat series of words in the same order as they were presented (Eysenck & Keane, 2015; Shing & Lindenberger, 2011).

4.2.1 Episodic-like memory in animals

Episodic memory is present and well established in humans but difficult to test in animals given that they cannot verbally report their subjective experiences. It has not been unequivocally proven that episodic memory has evolved in species other than humans (Thorpe et al., 2004). When studying humans, the measured behaviour is often communicated verbally. It is presently not resolved how to formulate clear behavioural criteria for animal studies to describe those processes that are usually reported verbally and via imaging in humans (Shettleworth, 2001). It is possible to study the ways animals acquire information about their world and their responses to them, but the study of their possible ‘consciousness’ always meets a seemingly unsurmountable problem: we cannot know whether the animals are consciously (re)experiencing because we cannot question them about their experiences. Episodic memory stores personal past events and the recall of episodic content requires re-experience of that past event and therefore a need to travel back to that point in time in a conscious manner (Martin-Ordas et al., 2010; Tulving, 1983, 2005). It is suggested that episodic memory is critically dependent on the concept of self. To be capable of relating memory representations to experiences of one´s self in the past one would need an awareness of self in the present time too (Howe & Courage, 1993).

The former definition of human episodic memory makes it extremely difficult, if not impossible to demonstrate this type of memory in animals. For animals, we therefore refer to the phenomenon as ‘episodic-like memory’. Episodic-like memory was firstly defined by Clayton and Dickinson (1998) who suggested that it needs to meet the behavioural criteria of *what-where-when* (WWW paradigm). The first evidence of what-where-when memory in non-humans was provided by the classic experiment on scrub jays (Clayton & Dickinson, 1998): these birds store their food for later recovery when it is needed. The jays were given two kinds of food for caching, fresh worms and nuts. Fresh worms are preferred by the jays but decay after a certain period of time while nuts remain in good conditions for a very long time. When the birds were allowed to retrieve the food items after a short period of time since caching, they selected the worm caching site. In contrast, if the time interval was long, the scrub jays chose to retrieve caches from the nut location.

With this experiment, Clayton and Dickinson (1998) showed for the first time that an animal species, scrub jays, could remember what, where and when. However, it was argued that food caching and retrieval behaviour is very likely genetically fixed hence lacking conscious recollection of those memories (Zentall, 2010). Also, humans have semantic memories such as historical events that include information about what happened, where and when and episodic memories that do not include all those three components (Eysenck & Keane, 2015). The WWW paradigm failed to provide evidence of the autonoetic or conscious components of episodic memory found in scrub jays, and therefore their ability was called episodic-like memory (Suddendorf & Corballis, 1997, 2007).

This experiment was later adapted to rats by (Babb & Crystal, 2005, 2006a, 2006b). Rats were trained in an eight-arm radial maze. Each arm had a small piece of food at the distal end and the rats could explore the maze and consume all the food. The optimal strategy for the subjects would be to visit each arm just once since no additional food was available after consumption. Rats performed at near-optimal level using their memory for recently visited locations. Until today, this kind of WWW memory has been shown in species ranging from rats to cuttlefish and successfully remembering that type of food is located where and available when (Crystal, 2021).

Another approach to test for episodic-like memory in animals is by conducting unexpected recall tests. Zentall (2010) have argued that many paradigms investigating episodic-like memory require extensive training producing expectations in the animals being tested. It is therefore impossible to exclude semantic-like knowledge as an explanation for the behavioural responses, or prepared behavioural responses generated from a planned action (Crystal, 2021). The explicit training for the contingencies in food availability inspires the development of semantic knowledge during the experiments

(Crystal, 2010). Zentall (2010) proposed that episodic-like memory can be documented when an animal reports a recent event when there is no expectation that this report would be required, which could be compared with answering an unexpected question in humans.

Using this so-called ‘unexpected question procedure’, Zentall et al., (2001) trained pigeons in a symbolic match-to-sample task where pigeons were presented with two stimuli to signal a particular behaviour: vertical lines for pecking and horizontal lines for not pecking. The stimuli were then followed by a red and green key. A food reward was given both when the pigeons pecked the green key following a pecking stimulus (vertical lines) and the red stimulus following a non-pecking stimulus (horizontal lines). To formulate a correct response and therefore, earn a food reward, the pigeons were required to recall what was the previously presented stimulus and how they reacted to it. This experimental set up allowed the pigeons to effectively report their past actions but as the delays were so short, the results of this experiment could also be explained in terms of working memory (Dere et al., 2006; Fugazza et al., 2020). Recently, a study of dolphins tested their episodic-like memory using the ‘unexpected question procedure’. During this experiment, dolphins were trained to retrieve a ball from one out of two trainers. In the experimental phase, the dolphins were asked to retrieve the ball from a particular location (the ‘Where’ condition) from two possible locations, or trainer (the ‘Who’ condition) from two possible trainers. After a delay of 10 minutes, a single trial was conducted where the dolphins were sent to retrieve the ball, but the ball was absent, which was considered as unexpected. In the ‘Where’ condition, the dolphins went to the location where the ball was previously located 10 minutes before whereas in the ‘Who’ condition, the dolphins went to the trainer that was holding the ball 10 minutes before. The authors argue that, in the unexpected absence of the ball, the dolphins remembered their previous experience and therefore repeated the scenario that they experienced 10 minutes before.

It has also been proposed that the ability to remember the temporal order of events is a critical feature of human episodic memory (Roberts, 2002). Rats have been tested for this type of memory and shown to remember the temporal order of odours (Agster et al., 2002; Fortin et al., 2002) and object sequences (Hannesson et al., 2004; Mitchell & Laiacona, 1998).

Other animals have been tested for episodic-like memory such as non-human primates (Schwartz et al., 2005; Schwartz & Evans, 2001), Meadow voles (Ferkin et al., 2008), rats (Babb & Crystal, 2006a; Eichenbaum et al., 2005), cuttlefish (Jozet-Alves et al., 2013) among others. Even though all these studies found evidence for episodic-like memory, most of them can be interpreted differently in terms of familiarity of the task or semantic knowledge rather than episodic memory. To qualify as a clear case of episodic memory, test subjects must not expect that they will have to recall an experienced event in the future (Zentall, 2010). Most tests so far however, repeatedly exposed the subjects to the same test scenario, in which responding to a certain situation depending on the past was rewarded. It can therefore not be excluded that the animals learned what knowledge was required in a certain test scenario, thus eliminating the need of travelling back to a particular episode in time (Zentall, 2010).

Suddendorf & Busby (2003) suggested that evidence for episodic memory subjective time travel in nonverbal organisms could take the form of the re-enactment of events through expressing or represent them, also known as pantomime. An animal’s ability to recall its own behaviour is a method to determine its’ level of consciousness. This method has been used in pinnipeds, pigtail macaques, dolphins and dogs (Fugazza et al., 2020; Mercado et al., 1998; Paukner et al., 2007; Scagel & Mercado III, 2022; Smeele et al., 2019). Even though all animals were trained to understand the abstract rule of repeating their previous behaviour, little detail was given for the monkeys, the dolphins and the dogs regarding their training process and previous experience, making comparisons between species difficult.

In recent years it has been proposed that it would be more productive to test for the capacity to form mental representations and for prerequisites and subcomponents of episodic memory rather than find a paradigm that would prove truly episodic memory in animals (Templer & Hampton, 2013). The question would then shift from "do animals exhibit episodic memory?" to "what aspects of human episodic memory are present in animals?". It has been suggested that the main prerequisites for episodic memory are:

- Metacognition: awareness of own knowledge, perceived experiences and memories.
- Conscious recollection: ability to spontaneously report a previously personal experience.
- Temporal order memory: a sense of subjective time.
- Mental time travel with prospective and retrospective cognition: requires the concept of the self to mentally travel into owns personal past and plan or imagine the future.

A unique and restricted conception or definition of episodic memory would ignore the fact that episodic memory might have evolved differently in different species, as a result of species-specific socio-ecological demands (Templer & Hampton, 2013). Instead, identifying interesting and more informative specializations of memory in different animals, without the restrictions of categorizing them, might make memory research in animals easier. The interest in future planning abilities and memory for the future has grown within the scientific community since episodic memory must have evolved to promote adaptive behaviour in the present and in future (Shettleworth, 2009). Researchers are starting to develop prospective memory tests for animals to study future planning as the neural systems for mental simulations of future events and episodic memory are the same for humans (Schacter et al., 2012; Templer & Hampton, 2013).

4.3 Prospective memory

Prospective memory is a subtype of episodic memory and therefore considered long-term memory (Figure 3; Table 1). Prospective memory is the process of remembering to do something at a specific time in the future. The intention or action cannot be performed at the present time but must be maintained across time until the proper opportunity at the appropriate time (Einstein and McDaniel 2005; McDaniel et al. 2004; Perdue et al. 2014). The action intended to be performed in the future, needs to be maintained either consciously or unconsciously (Perdue et al. 2014).

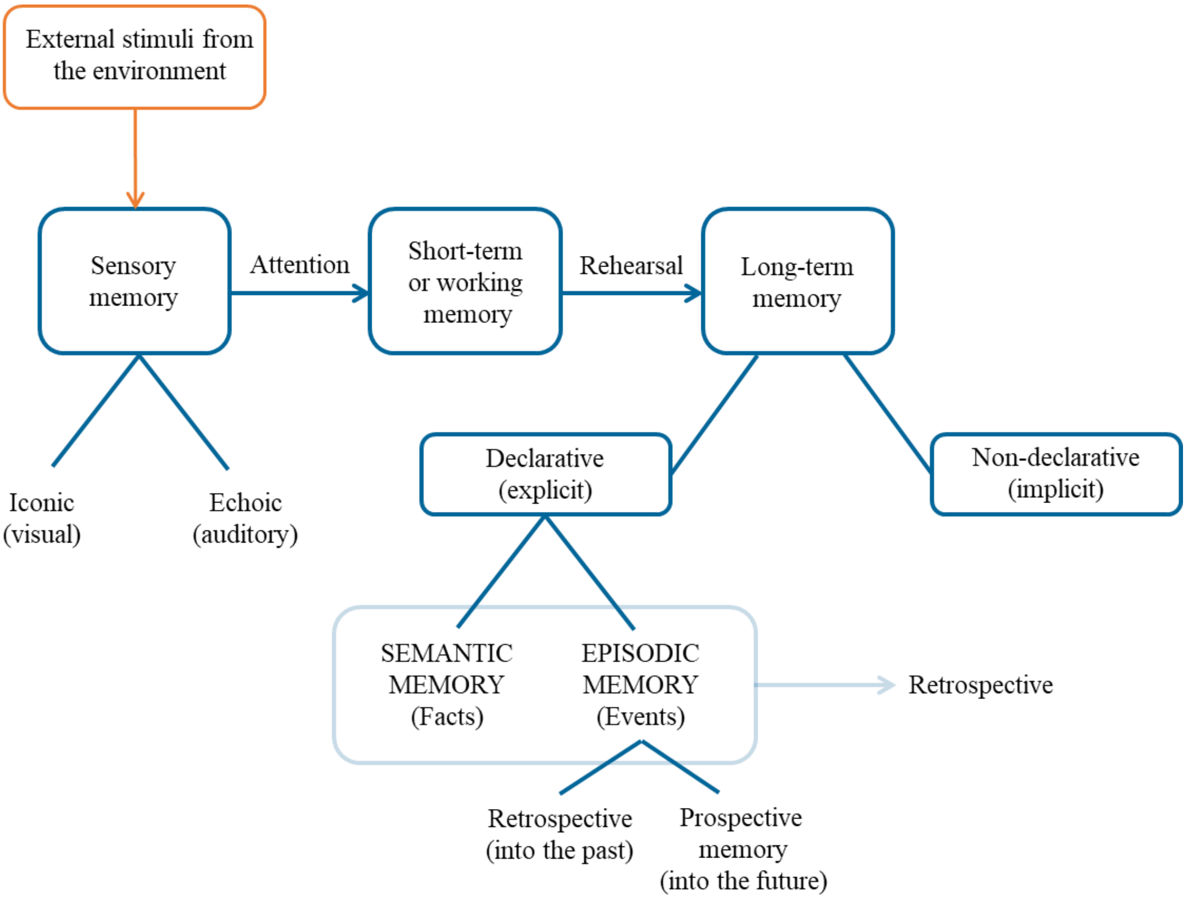


Figure 4. *Types and subtypes of memory described in the present thesis.*

The term ‘prospective memory’ refers to the ability to plan, retain and recall an intention to perform an action in the future from memory, without an overt signal or cue to remind the individual to perform the action (Cohen & Hicks, 2017). Prospective memory is therefore defined as the set of abilities that allow us to remember to perform a specific intended action in a specific temporal moment (Crystal, 2013). This type of memory is crucial for humans to organize their time and realize their goals . Failures in prospective memory are often not important, but in some situations, the consequences can be dramatic (Einstein & McDaniel, 2007; Haas et al., 2020), such as forgetting to turn off the oven, or leaving a dog on the back seat of the car on a warm day. Prospective memory focuses on an action to be carried out the future and is closely related to retrospective memory, which focuses on the past.

4.3.1 Prospective and retrospective memory

While prospective memory is about remembering to do something in the future without being reminded externally of doing it, retrospective memory is about remembering something that happened in the past (McDaniel & Einstein, 2007). If someone asks, what you had for breakfast, the question will elicit recalling that specific memory. Semantic memory, episodic memory and procedural memory are considered retrospective (Baddeley et al., 2009).

Another difference between prospective and retrospective memory is that prospective memory revolves around the “when” we need to perform the action, while retrospective memory focuses on the “what” we know about something (Anderson, 2005). Even though prospective and retrospective are different types of memory, they are not independent, because if we have the intention to perform an action in the future, but we cannot recall what action we are supposed to do, our prospective memory fails. Crawford and colleagues (2003) developed a 16 questions questionnaire (PMRQ) to evaluate prospective and retrospective memory. The analysis of the factorial structure of this questionnaire indicated that the best model fitting the obtained results was formed by three factors: general episodic memory, prospective and retrospective memory (Figure 4). All the elements of the questionnaire contributed to episodic memory while some elements contributed only to prospective memory and the rest of the elements, to retrospective memory. The three-factor model also fits the idea that prospective memory and retrospective memory cannot be completely dissociated (Rönnlund et al., 2008).

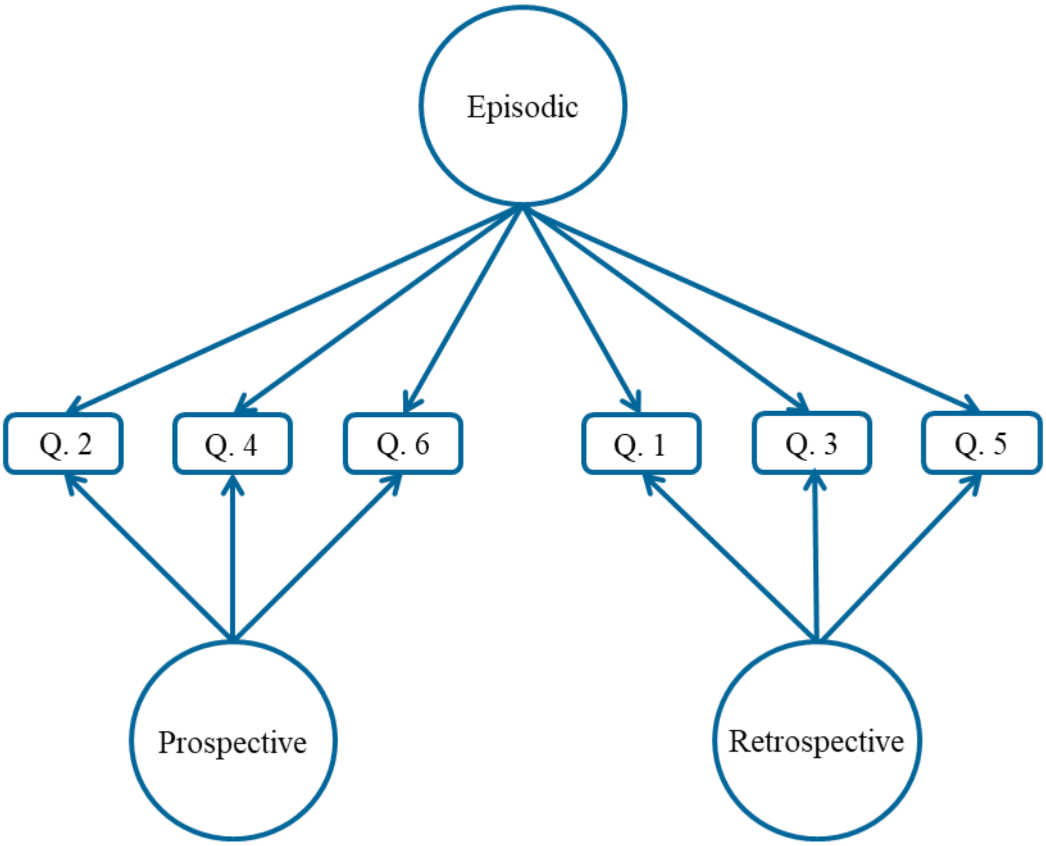


Figure 4. *Schematic description of the competing three-factor model of the latent structure of the Prospective-retrospective memory questionnaire (PRMQ). The boxes containing the Q. # between episodic and prospective/retrospective memory represent a question of the questionnaire. The real representation has 16 boxes but in this case it was simplified to 6. From: Rönnlund M., Mäntylä T., Nilsson L. (2008).*

4.3.2 Types of prospective memory

Current research in prospective memory distinguishes between two different types: event-based prospective memory and time-based prospective memory. Time-based prospective memory requires the individual to remember the task to be performed at a very specific moment in time (e.g., going to a job interview at 10 a.m.). Event-based memory involve remembering to perform a specific action under the appropriate circumstances (e.g., buying milk in the supermarket on the way home from work;)(Sellen et al., 1997). Both types of prospective memory include the three typical stages of all the memory processes: Codification, retention, and recall, but, in addition, two extra stages: Execution and evaluation.

(i) Codification or encoding: The codification is the process in which the intention to perform a future action is formed.

(ii) Retention: The retention refers to the storage duration of the intention, and the retention duration can vary. During the retention interval, the subject is usually engaging in activities that are not related to the action to be remembered.

(iii) Recall or retrieval: The recall starts when the individual, in a conscious manner, recovers the intention to perform the programmed action from their memory.

(iv) Execution: When the intention is retrieved, the individual needs to act upon it.

(v) Evaluation: Finally, the outcome of the previous cited stages needs to be evaluated. If there is a failure in prospective memory, the subject needs to replan it.

4.3.3 Prospective and retrospective memory in animals

As memory is crucial for planning for the future, before reviewing experiments in prospective memory in animals, it is important to differentiate between different mechanisms by which animals can perform future-oriented behaviour. Even though much animal behaviour have consequences for the future, not all future-oriented behaviour requires a sense of the future. Such behaviours future unaware behaviours are underpinned by fixed action patterns and learnt associations (Figure 5). In contrast, three types of future-oriented behaviours that do require sense of the future have been proposed: prospective memory, semantic future thinking, and episodic future thinking (Raby & Clayton, 2009).

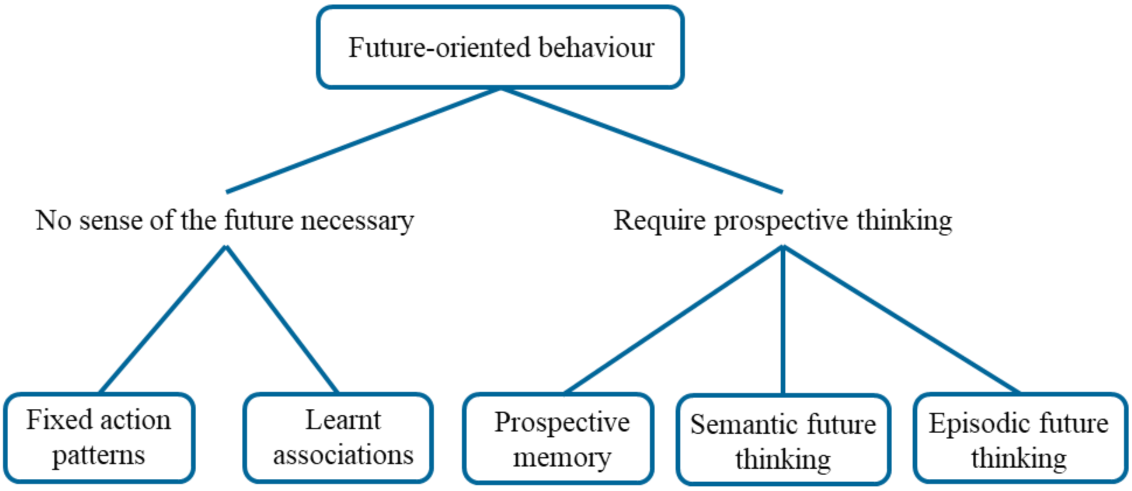


Figure 5. *Proposed behavioural categories for future-oriented behaviour (From* Raby & Clayton, 2009)

- Fixed action patterns: the behaviour is triggered by external cues, such as temperature or season variation. Hibernation, nest building or migration are examples of fixed action patterns (Raby & Clayton, 2009)
- Learnt associations: the behaviour is a consequence of stimuli being reinforced or punished, also called "classical conditioning". A typical example are Pavlov's dog salivating with the sound of a bell when the bell was paired with food rewards (Bitterman, 2006).

- Prospective memory: in animals it refers to their use of short-term memory in tasks with a delay between the stimuli and the opportunity to give a response (Raby & Clayton, 2009).
- Semantic future thinking: refers to the ability to mentally represent scenarios that do not necessarily involve oneself in the future. The concept of future is semantic (Raby & Clayton, 2009).
- Episodic future thinking: in this case, the projection into the future is personal. Therefore, oneself is part of the imagined future scenario and therefore is episodic in nature (Raby & Clayton, 2009)

The evidence for prospective thinking in animals derives from experiments in self-control, anticipation, goal-directed behaviour and future planning (Raby & Clayton, 2009).

In self-control tasks, typically, animals need to ignore an immediate reward in order to obtain a larger reward after a short period of time (delayed gratification). Theoretically, knowing that a better reward is coming in the future will prevent the animals from taking the immediate food reward. This method is not widespread as a valid form of testing for future thinking because choosing an immediate gain could be the most adaptive strategy when foraging for certain species, like for example, a carnivore that does not have the opportunity to eat that often, and may not necessarily reflect the animal's inability to predict or anticipate the future (Raby & Clayton, 2009).

In anticipation tasks, animals show that they expect a future event to occur. Here, the main challenge is to discern between real anticipation and associative learning explanations.

Goal-directed behaviour, which implies prospective thinking, has been shown in apes, e.g., when anticipating which tools they require to solve a novel problem would sharpen sticks to use as tools for termite fishing. The main criticism of goal-directed behaviour is that all experiments involve food, so the own hunger motivational state of the animal can motivate the goal-directed behaviour.

Studies on future planning need to prove a dissociation between the subject's present mental state from the one that is predicted in the future. That is, that an animal that is not hungry in the present moment, should be able to think that he might be hungry and the future and therefore, it is convenient to execute a particular behaviour for when the hunger moment comes (Raby & Clayton, 2009; Suddendorf & Corballis, 1997).

Prospective memory has been tested in chimpanzees and rats using naturalistic approaches (Cook et al., 1985; Perdue et al., 2014) but also experimental ones (Martin-Ordas et al., 2010). In one of the experiments, rats learned to visit all the arms in a radial maze without duplication. To perform this task, they could use either retrospective memory, which would include the rats using a representation of the arms they had already visited or in terms of prospective memory, by using a representation of the arms still to be visited. In an eight arms radial maze, the probability of error increased when the number of visited arms was four. For more visits, the error decreases again (Cook et al. 1985). Chimpanzees were presented with two food items and had to choose one of them. The second one would then be stored in a box while the tested chimpanzee was watching. Then, the animals started a *quantity judgment task* lasting eight minutes that was used as "distraction", were subjects had to choose the container out of two with more food items. After the task, if the chimpanzees used their prospective memory to remember that the food was stored in the box, then they would ask for the retrieval of the food item spontaneously. Chimpanzees did ask the researcher about the food item by pointing at the box or by using other clear signals suggesting that they remembered their intended action and show some kind of prospective recollection. Chimpanzees performed better than three year-old children since they did not need any cues to remember the hidden item after a time delay (Perdue et al. 2014). Prospective memory has also been tested using computerized tasks in which monkeys were trained for a match-to-sample task (Evans & Beran, 2012). The task consisted of moving a cursor to a previously matched item. The authors inserted a psychomotor tracking task before the monkeys had the opportunity to match, and this enabled the authors to visualize how the monkeys were preparing for their future response.

Thorpe and colleagues (2004) concluded that the experiments on prospective memory so far could not be considered as unequivocal tests of prospective memory because the context of the task in these experiments explicitly prompted remembering. Instead, these experiments were only measuring the animal's capacity to retain to-be-performed tasks. The to-be-performed behaviour mediated by interval timing mechanisms is commonly found in many animals (Gibbon et al., 1984; Shettleworth & Hampton, 1998), one example would be when hummingbirds remember to revisit flowers at the rate at which they regenerate nectar (Gill, 1988). The so-called Bischof-Köhler hypothesis states that future planning requires the anticipation of motivational states that are not experienced in the present moment (Paxton & Hampton, 2009). To our knowledge, future planning as defined by the Bischof-Köhler hypothesis has not yet been proven in animals for two main reasons: first, because prospective cognition requires anticipation over a time scale of hours, or longer (Clayton et al., 2003), and secondly, because the tasks used so far involve the use of food, which means that the motivational state of hunger in the tested animal cannot be ignored.

In a typical prospective memory task, humans are instructed to do something later in the experiment, when encountering a certain cue. Until the cue is presented, they are typically engaged in distracting activities. Successful prospective memory use occurs when subjects respond to the cue in the relevant manner following the earlier instructions. So far, asking an animal to actively remember a specific action that will be required in the future has not been possible and only humans have been tested under such conditions.

5. Forgetting

Forgetting was defined by Tulving (1974) as the inability to recall something that could be recalled on an earlier occasion. In the 20th century, the dominant approach to forgetting was interference theory (Eysenck & Keane, 2015). According to this theory, our current learning can be interfered with previous learning, also denominated proactive interference, or future learning, known as retroactive interference. Proactive interference can be useful when things change in the environment and old knowledge is no longer needed. Retroactive interference, on the other hand, is generally useful when new learning resembles previous learning. An example of retroactive interference would explain why people forget some of their first language when learning a new one.

One of the best-known theories of forgetting is called repression and was developed by the psychologist Sigmund Freud (Freud, 1957). Repression was defined as the inability to access frightening or traumatic memories. It has debated whether forgotten memories are completely erased or if they can be retrieved with specific cues. Some scientific evidence has shown that forgetting can be caused by a failure in retrieval rather than a complete erasure of the memory content (Delaney et al., 2009).

Delaney et al. (2009) have demonstrated the existence of directed selective forgetting. This effect can be explained by the available attentional resources and the selective demands imposed by the experimental task. Motivated or intentional forgetting can be adaptive in terms of cognitive economy, for example, by reducing proactive interference. 'Directed forgetting' is a phenomenon caused by the instruction to forget some information that is being presented for learning (Tulving, 1974). Directed forgetting is important since the suppression or repression of memories occurs in a deliberate manner, consciously, and not automatically as Freud suggested. Directed forgetting is just one way in which forgetting occurs, as most forgetting occurs in spite of our efforts to remember.

Most often, forgetting occurs by the lack of appropriate cues to retrieve memories. Forgetting can in these situations be considered to be cue-dependent. The cues can be either internal or external. However, to generally describe forgetting in cue-dependent terms is complicated. To modelled forgetting over time, 'consolidation theory' provides an explanation of the form of the forgetting curve (Meeter & Murre, 2004). Consolidation is a process that fixes information in long-term memory for long periods of time (possibly years). Consolidation involves two major phases: the first occurs over a period of hours, and the second, over a period ranging from days to years. This second phase applies exclusively to episodic and semantic memories.

Table 1. *Table summarizing all types of memory explained in the present thesis, the criteria for their classification, and in which studies are involved.*

Memory type	**Criteria**	**Duration**	**Equivalent in animals**	**Studied in this thesis**
Sensory memory	Every stimuli perceived by the senses	Less than 1 s	Sensory memory	-
Short-term memory	Preserves small quantity of information for a short period of	Less than 30s*	Short-term memory or working	Study 2 and 3

	time		memory	
Long-term memory	Preserves large quantity of information for a long period of time	From a few minutes to a lifetime	Long term memory	Study 1
Declarative memory (explicit)	Long-term memory for descriptive information	From a few minutes to a lifetime	Explicit memory	Is needed for the experiments but not discussed
Non-declarative memory (implicit)	Long-term memory for perceptual, cognitive and motor skills	From a few minutes to a lifetime	Implicit memory	Is needed for the experiments but not discussed
Episodic memory	Declarative long-term memory of personal experiences	From a few minutes to a lifetime	Episodic-like memory	Study 1, 2 and 3
Semantic memory	Declarative long-term memory for generalized concepts	From a few minutes to a lifetime	Semantic memory	Alternative explanation for Study 1, 2 and 3
Prospective memory	Subtype of episodic memory for future intentions	From a few minutes to a lifetime	Prospective memory	Study 1
Retrospective memory	Long-term memory referred to past events. Includes episodic and semantic memory	From a few minutes to a lifetime	Retrospective memory	Study 1, 2 and 3

6. Memory for actions and the repeat paradigm

Most of human everyday memories involve past actions, i.e., memories of what oneself or others did in the past (Zimmer et al., 2001). Such memories of past events involving past actions shape current behavior as well as guide future behavior (Goswami, 2013). Yet, most memory studies on humans and non-human animals are based on remembering passively presented stimuli, without overtly involving and often even restricting actions (Fujita et al., 2012; Lind et al., 2015; Zimmer et al., 2001). Besides involving overt motor behavior, actions are also different from the traditional passive stimulus presentation approach because they are self-performed (Fujita et al., 2012; Kuczaj, 2014; Lind et al., 2015; Zimmer et al., 2001). Given that the definition of human episodic memory (Tulving, 1972, 1985) is the “memory for personally experienced events” and that self-performed actions are per se “personally experienced”, memory of self-performed actions should be considered episodic accordingly. Being able to recall and represent one's own past actions is at the same time considered as of the main prerequisites or main “building blocks” for the ability to represent the self (Conway, 2005; Fugazza et al., 2020; Hauser et al., 2002). It has been speculated that it may have evolved early in mammalian evolution and could be widespread phylogenetically, since it has recently been documented in domestic dogs (Fugazza et al., 2020; Fujita et al., 2012; Scagel & Mercado III, 2022), as well as dolphins, primates and pinnipeds (Mercado et al., 1998; Paukner et al., 2007; Smeele et al., 2019). Given that self-representation in turn is a prerequisite for human episodic memory (Clayton, 2017), this applies to remembering one’s own past actions inevitably. As self-awareness of one's own personal experiences is not clearly proven in animals, the analogous memory processes in animals are often referred to as episodic-like memory (Clayton, 2017; Clayton et al., 2000). To date, several studies have reported evidence for episodic-like memory in a few animal species although most of them remain debated. For example Clayton & Dickinson (1998) claimed the first evidence for evidence for episodic-like memory showing that scrub jays (*Aphelocoma californica*) are able to remember where and when they have cached a particular food item and claimed it could imply the ability of episodic memory for the species. However, it was argued that food caching and retrieval behavior is very likely genetically fixed and the paradigm used failed to provide evidence of conscious (‘autonoetic’) components of episodic memory possible in a scrub jay (Tulving, 2005), thus, the ability was called episodic-like memory (Crystal, 2021; Suddendorf & Corballis, 1997, 2007).

Testing an animal’s ability to repeat its own previous behavior, i.e., the “repeat paradigm”, has been put forward as a method to determine animals’ memory for their own actions (Mercado et al., 1998; Mercado III et al., 1999) and recently has been proposed as a method of testing episodic-like memory in two studies on dogs (Fugazza et al., 2020; Scagel & Mercado III, 2022). The methodology has great potential as a comparative test for episodic-like memory content in animals, but the prerequisites for truly episodic-like memory retrieval rely on the assumption that the animals must not expect to be asked about the past event (Zentall, 2010). The unexpectedness of the test rules out a prepared behavioral response (i.e., the animal expects the trial and gets ready to offer the correct behavioral response rather than retrieving the past event from their memory) from the animal, instead of an episodic content retrieval (Fugazza et al., 2016, 2020).

To date, the “repeat paradigm” has been employed in pinnipeds, pigtail macaques (*Macaca nemestrina*), dogs and dolphins (*Tursiops truncatus;* Fugazza et al., 2020; Mercado et al., 1998; Paukner et al., 2007; Scagel & Mercado III, 2022; Smeele et al., 2019), i.e., four mammalian taxa. Even though all tested species learned to repeat their previous behavior on a range of behaviors they could perform on command, the extent to which the different species relied on the underlying repeat concept, i.e., “repeat your last action” remains unclear. Little detail was given for the monkeys, dogs and dolphins regarding the training procedure and previous experience, making comparisons between species difficult. In any case, dolphins and dogs were reported to generalize the repeat command to novel behaviors (Fugazza et al., 2020; Mercado et al., 1998; Scagel & Mercado III, 2022) and macaques were found to fail (Paukner et al., 2007) while pinnipeds were not tested (Smeele et al., 2019). Concerning the duration of memory retention, the species differed substantially, but given the methodological differences between the studies, one cannot directly compare these results and draw reliable conclusions from them.

7. Animal subjects

7.1 Parrots

Parrots belong to the order Psittaciformes and are a diverse group of birds, containing 398 species in 84 genera (Carballo et al., 2020; Del Hoyo et al., 1992; F. Lambert, 2014). They are also morphologically very diverse showing a remarkable range of sizes (from 8 cm to 1000 cm; Forshaw, 2010) and weight (from 10 grams to four kilograms; (Dunning Jr, 2007), display great variety of plumage colourations and are widely distributed throughout the tropics and subtropics of the world (Forshaw, 2010).

Parrots are an interesting model group for several reasons. As birds, they exhibit a great evolutionary distance to mammals, with which they share a common ancestor 296 mya (Osvath et al., 2014), but still they show many advanced social and cognitive traits usually thought as being ‘purely mammalian’ or even ape-like. Current evidence suggests that parrots parallel the great apes and primates in their cognitive abilities (Lambert et al.). Different parrot species show different social behaviour or foraging strategies. Generally, they are highly social animals that form monogamous couples and typically live in complex fission-fusion groups (Pitter & Christiansen, 1997; Toft & Wright, 2015). In this way they are similar to chimpanzees and dolphins, which show high levels of social complexity with often large social groups that are not stable in composition but experiencing constant interchange of group members between flocks. Another important life history trait of parrots in which they resemble great apes and dolphins is their longevity. Parrots are among the longest-lived birds (Smeele et al., 2022; Wasser & Sherman, 2010). The oldest recorded parrot, a Salmon-crested cockatoo (*Cacatua moluccensis*), was 92 years old (Young et al., 2012). Just like many mammals, parrots also have a slow development during ontogeny (N. J. Emery & Clayton, 2004) and thus likely depend on social learning from their parents and group members.

Their social complexity and the diversity of their foraging habits together with their longevity and slow development may have been important selection pressures acting on their cognitive abilities and may thus explain the impressive performance of parrots in cognitive tasks. Superior cognitive abilities seem to be adaptive for functioning as cooperative unit within their pair bond and may be required for maintaining complex social bonds (N. Emery et al., 2007). Maintaining valuable social bonds may require careful coordination and synchronisation, as well as special socio-cognitive adaptations, hence complex ‘relationship intelligence’ might be required (N. Emery et al., 2007). In fission-fusion societies (Toft & Wright, 2015) social intelligence may be important to recognise group structure in varying hierarchies and potential conflicts among the members of the flock. Regarding their feeding behaviour, parrots have diverse diets (Toft & Wright, 2015) that may require greater behavioural flexibility and high rates of feeding innovation (Lefebvre et al., 1997; Sol et al., 2002, 2005, 2007). Many parrots feed on unripe seeds, which can be toxic at certain quantities. Parrots then need to know in which seeds to forage and for how long to avoid toxicity levels (Bradbury & Balsby, 2016). Their diverse feeding habits may also explain their ability to use tools (Lefebvre, 2013; Shaw, 2021).

Another defining feature of parrots is that they are open vocal learners like dolphins, which means that they can learn new vocalizations throughout their lives. They produce signature calls unique for each individual similar to signature whistles on dolphins(Balsby et al., 2012). The functions of their vocal imitation ability and flexible calls may be that are important to their sociality for several reasons. Parrots show geographical variation in their calls, which might indicate that these are important for the flock maintenance of territories. Also, observations in the wild have shown a great exchange of calls during the formation of foraging groups (Bradbury & Balsby, 2016). Parrots are also well known for their rapid vocal imitation abilities, including the ability to mimic human speech. Perhaps the most famous example of vocal learning are the studies by Pepperberg (2007) on an African grey parrot (*Psittacus erithacus*) named Alex. This psittacine was able to label up to 50 different objects (using English vocalizations), and mastered relational skills such as ’equal to’ and ‘different’, as well as used phrases such as ‘Come here’ or ‘I want …’ in the right context, as a response to the scientist’s vocal questions. Thus, in the words of the author: ‘he [Alex] demonstrates intriguing communicative parallels with young humans, despite his phylogenetic distance’ (Auersperg & von Bayern, 2019; Pepperberg, 2002, 2007).

Lastly, because of their potentially long lifespan, parrots might have more opportunities to learn new calls, to explore their environment and innovate and to coordinate with their social partner than many other types of birds (or many species of mammals for that matter). They have potentially more time to learn and solve novel problems/innovate by using their greater cognitive abilities throughout their long lives (Auersperg et al., 2014; O’Neill et al., 2021; Scarl & Bradbury, 2009).

Considering all the above-mentioned features, it is not surprising that parrots also have specialised brains. Parrots and corvids possess a brain-to-body-size ratio that is comparable to that of primates (N. J. Emery & Clayton, 2005a). Their brain is therefore large relative to their body size (Iwaniuk et al., 2005) and extremely densely packed with neurons (Olkowicz et al., 2016). More specifically, they have an enlarged pallium relative to the rest of their brain (Iwaniuk et al., 2005). The pallium is the comparable brain structure to the mammalian cortex and is the region thought to be responsible for complex behaviour and high cognitive processing (Güntürkün, 2005; Jarvis et al., 2005). Since bird brains do not have a densely layered and connected cortex, complex cognition was thought to be beyond them. However, the pallium in parrots is highly interconnected and densely packed with neurons that act like the layered regions of the cortex but organised differently (Güntürkün & Bugnyar, 2016). In parrots, it seems like these regions might have executive control functions as they have a greater connection to other lower regions in their brain (Gutiérrez-Ibáñez et al., 2018). Comparing parrots with other species of birds, the Psittacidae family have larger and more densely packed and connected pallial regions, therefore it is not surprising that they show higher cognitive abilities and vocal capacities (Herculano-Houzel, 2017). Apart from their densely neuron-packed brain, avian brain neurons are highly efficient consuming three times less glucose than mammalians (von Eugen et al., 2022).

For the experiments in the present thesis, I chose the blue-throated macaw (*Ara glaucogularis*). Because most macaw species live in dense rainforest in South-America, very little is known about their natural behaviour. Blue-throated macaws are endemic to small areas of the western Amazon basin in Bolivia and they are globally threatened (Herzog et al., 2021; Tassin de Montaigu et al., 2020). They generally live in long-term pairs but have also been observed in family flocks. Blue-throated macaws mainly eat fruits from large palms (Yamashita & de Barros, 1997). Cognitive studies have shown blue-throated macaws being able to cooperate in the lose-string task, where two parrots need to pull a string simultaneously to bring a sliding board with food into reach, even though they did not seem to understand the role of their partner (Tassin de Montaigu et al., 2020). They are also capable of self-control, temporal discounting and economic decision making and can solve problems with using different tools (Kabadayi et al., 2017; Krasheninnikova et al., 2018; Krasheninnikova, Berardi, et al., 2019; O'Neill et al., 2019, 2020, 2021). To my knowledge, no studies on memory have been performed on parrots to this date, but their trainability, cognitive abilities and complex communication systems, makes parrots a perfect animal model for this project, and given the multiple socio-ecological and cognitive parallels to dolphins, they form an interesting comparison to them.

7.2 Dolphins

The species used for the studies presented in this thesis in the bottlenose dolphin (*Tursiops truncatus*). These animals are large and can reach a length of over 4 meters and a weight ranging from 150 to 650 kg (Kastelein et al., 2003). Their colouration is often dark grey on the top, and lighter grey on their ventral part as a form of camouflage. Bottlenose dolphins are cosmopolitan members belonging to the family Delphinidae (Hoelzel, 2009). They are distributed worldwide except for the Arctic and Antarctic regions (Wursig & Perrin, 2009). Their mating system is defined as hierarchical promiscuous, meaning there are no strong pair bonds between individuals and mating is determined by dominance (Connor et al., 2000).

Similar to parrots, dolphins share many of the features believed to be associated with advanced cognitive skills, such as high sociability, longevity and slow development during ontogeny (N. J. Emery & Clayton, 2004).

Dolphins are ideal animal models for this project for different reasons. Firstly, dolphins are excellent problem solvers and are famous for their cognitive abilities, including tool use (Krützen et al., 2005; Mann et al., 2012; Marino et al., 2007; Smolker et al., 1997). Dolphins possess the highest brain to body size ratio after humans and above chimpanzees (van Horik & Emery, 2011; Van Horik et al., 2012) and high neuron density in their brains (Ridgway et al., 2019). In addition, the dolphin neocortex is characterized by a high ratio of glial cells to neurons (Marino et al., 2007) suggesting a high degree of interconnectivity. Dolphins also exhibit complex communication systems and use signature calls to address individuals (Bruck et al., 2022; King & Janik, 2013; Richards et al., 1984). Like parrots, they are open-ended vocal learners and have a great ability to imitate vocalizations even from other animal species. Dolphins have also shown syntax comprehension (Kako, 1999). They live in individualised societies in which individuals recognise and know each other (they are even known to remember individuals after being separated for over 15 years; (Bruck, 2013)).

Dolphins exhibit complex fission-fusion social systems (Lusseau, 2003) and remembering conspecifics could help recognize and avoid potentially aggressive individuals, help dealing with social conflict situations, avoid inbreeding, find hunting alliances or determine whom to give resources and whom to avoid (Bruck, 2013; Sayigh et al., 1995). Their groups sizes vary from 2 to 100 or even over a 1000 individuals (Orbach et al., 2014; Quick & Janik, 2008). Recent observations over several years in Shark Bay, Australia have shown that male dolphins cooperate forming long-term but also dynamic alliances in order to sequester and consort females for mating (Gerber et al., 2022; Wild et al., 2019). Second order alliances are formed by 4-14 male dolphins which constitute the core social unit. From the second order alliances, 2-3 males form a first order alliance, who are the individuals who cooperate to sequester females for mating. Social bond strength between individuals will influence which males would form the first order alliances. Even though third-order alliances have been reported, males will rarely associate with other males creating third-order alliances (Gerber et al., 2020; King, Connor, et al., 2021).

Dolphins also exhibit “cultural traditions” by acquiring new behaviours from conspecifics that then spread throughout a population (Mann et al., 2012; Whitehead & Rendell, 2014). For transmission of culture to work, the information needs to be stored over time and the animals must use it when needed, but the existence of long-term memory has not been proven under controlled experimental conditions. Observations in Risso’s dolphins seem to show that these dolphins are able to plan foraging dives based on previous memories from prey distributions (Arranz et al., 2018).

Dolphin short-term memory for different stimuli has been investigated. The stimuli used ranged from sounds (Herman & Gordon, 1974; Herman & Thompson, 1982), visual materials (Forestell & Herman, 1988; Herman et al., 1989), self-performed behaviours, behaviours performed by other dolphin (Mercado et al., 1998; Xitco Jr, 1988) and spatial location (Thomson, 1976). Episodic-like memory was also recently, while wrapping up this thesis, reported in bottlenose dolphins using a paradigm to capture incidental encoding of a past experienced event (Davies et al., 2022). In this study, dolphins were trained to retrieve a ball from one of two available trainers. After a delay of 10 minutes, the dolphins were asked to retrieve the ball with the ball being absent. Dolphins went to the position where the ball was 10 minutes before in the “where” condition, or, to the trainer having the ball 10 minutes before in the “who” condition. An alternative explanation to the results found in this study is that the dolphins may be using reference memory. In this case, as there is no ball, and there is no ‘correct’ position, the dolphin goes to the previously reinforced location/trainer (Templer & Hampton, 2013). Yet, to date, there are no studies on long-term memory for action events or self-performed behaviour in dolphins.

8. Bayesian inference as statistical test

For the statistics I used Bayesian inference. Here a model contains prior information, data and parameters (Box & Tiao, 2011). For each parameter a prior is set. E.g., if a response variable can only increase with time, the slope parameter can be given a prior of exponential (1), meaning that values can be drawn from an exponential distribution with rate = 1. If a response variable can increase and decrease with time, but we expect the effect to be no greater than 2 per time-step, the prior can be set to normal (0, 1), which means that values greater than 2 or smaller than -2 are very unlikely, a priori. This give a clear advantage over frequentist models, which assume that any effect is possible, no matter how absurd. The result of the Bayesian model is a posterior distribution or density, which is the product of the prior with the likelihood (how likely is it that the datapoints came from parameter value x, y or z). The posterior distribution thus shows the range of values that are possible given the prior, data and model constraints. If, e.g., the mean of the posterior for the slope is well above zero, and very little mass is on the negative values, one can confidently state that there is a positive effect. For more complex outcomes it’s useful to show the combination of parameters from the posterior. A simple linear model would have a parameter for the intercept and for the slope. To show the variability on both we have plotted 20 samples from the posterior distribution for both variables. This leads to 20 different lines rather than one ‘mean’ line and a shade area. The advantage is that you can clearly see where the uncertainty comes from: if lines all slope the same, but have different intercepts, the model is more confident about the slope than about the intercept (Ellison, 2004). This information is often lost in frequentist models (Austin et al., 2002).

9. General relevance of the project for the broader field of research

Studies of memory have focused mainly on what animals remember about external stimuli, such as delayed matching-to-sample and food availability at different locations (Fujita et al., 2012; Lind et al., 2015) and less on what animals remember about internal stimuli, such as those related to their own experiences or actions (Mercado et al., 1998; Scagel & Mercado III, 2022). Fugazza and colleagues (2020) recently proposed that assessing a species' *ability to repeat a previous self-performed behavior* is a valuable comparative paradigm to investigate the evolution of both self-awareness and episodic-like memory (Suddendorf & Corballis, 1997). Concerning humans, episodic memory refers to the memory for personally experienced events, such as someone's first day of school, or a friend's birthday party, and thus requires the ability to represent the self mentally (Tulving, 2005).

The ability to remember one's own previous actions is a pre-requisite for and strongly relates to episodic-like memory, hence remembering and re-experiencing a past personally experienced event, because of the fact that the remembered actions had been self-performed, which per definition involves the self. The cognitive capacity to mentally represent situations or actions in the past or imagine possible future ones, enables humans to experience situations or visualize things that do not exist any longer or do not exist yet (McKellar, 1957; R. J. Sternberg, 1996). The study of mental self-representation in animals is challenging due to the difficulties to develop methodology relevant for the animals being tested. Whether animals have a concept of self is a complex topic difficult to be tested in animals (Clayton, 2017; Shettleworth, 2001). Traditionally, the main method used has being the mirror self-recognition test. This test was applied to a wide variety of species, from mammals to fish (Kohda et al., 2019; Plotnik et al., 2006; Reiss & Marino, 2001). However, the test is only revealing the visual recognition of one's own imagine, which can be considered only one aspect of self-representation (Suddendorf & Butler, 2013). It can be assumed that one of the building blocks of the ability to represent the self could be the ability to mentally represent own actions (Conway, 2005; Fugazza et al., 2020).

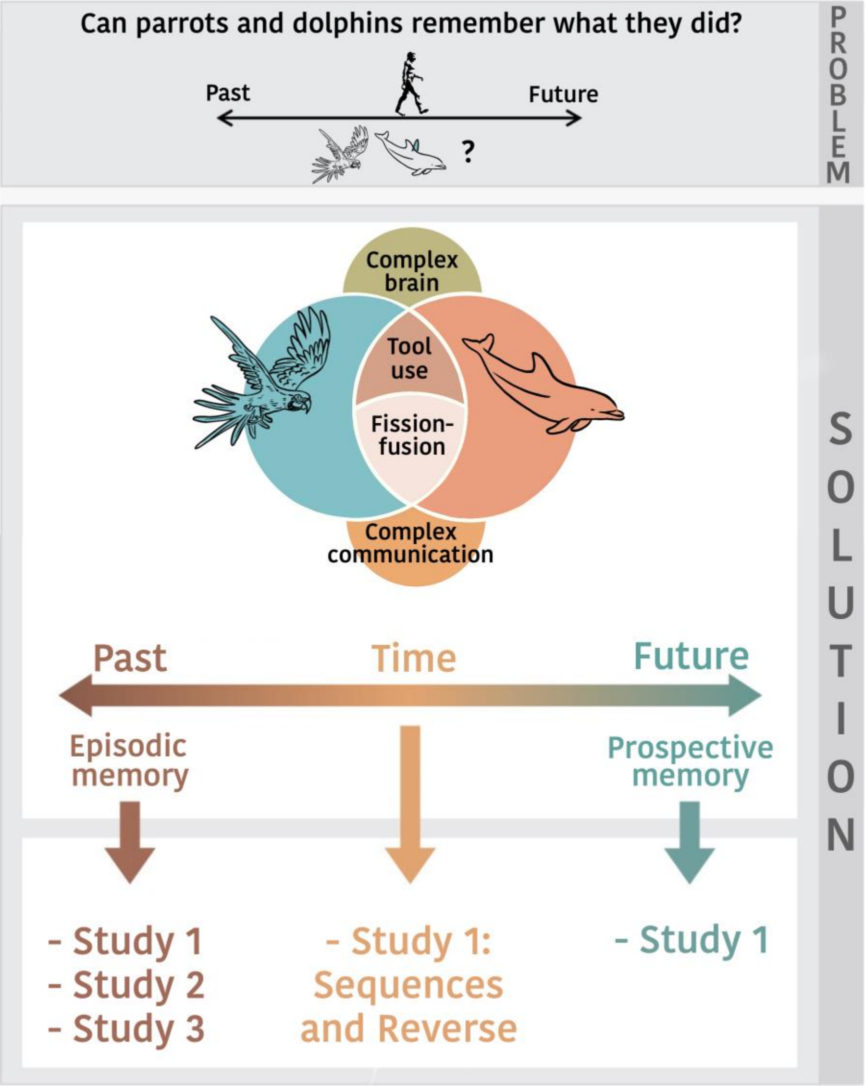


Figure 6. *Schematic representation of the aim of the present thesis and the proposed solutions.*

There are no studies on long-term memory for self-performed actions in dolphins. For parrots, no studies on memory have been performed until now, but their trainability, cognitive abilities and complex communication systems, make parrots an ideal animal model for this project, and given the multiple socio-ecological and cognitive parallels an interesting comparison to dolphins.

In the first study of this thesis, I tested bottlenose dolphins in a long-term memory task (Figure 6). Remembering to perform actions in the future enable humans to plan and realize goals (Walter & Meier, 2014) and involves active encoding of information for future use (Martin-Ordas et al., 2014; Ullman, 2004). We consciously form intentions, e.g., when planning our day and, as part of it, envision and order our future actions. Thereby, we know what we need to remember doing in the future and actively memorize our mental intended “to-do-lists” to ensure we recall what to do in the right situation. So-called prospective memories are a subtype of episodic memories that are used when an intention is formed to carry out an action, and when this intended action needs to be encoded and recalled at an appropriate moment in the future (Einstein & McDaniel, 2005; McDaniel et al., 2004; Perdue et al., 2014). Prospective memory is a complex process that involves other aspects of cognition and other types of memory, such as attention, executive control of cognitive function, and planning, but also episodic and retrospective memory (Crystal, 2013; Raby & Clayton, 2009; Thorpe et al., 2004). Prospective thinking requires a sense of the future, but not all future-oriented behaviours found in animals need the sense and understanding of a future (Raby & Clayton, 2009; Figure 5). Human prospective memory can be readily tested in the lab. In a typical prospective memory task, humans are instructed to do something later in the experiment, when encountering a certain cue. Until the cue is presented, they are typically engaged in distracting activities. So far, asking an animal to actively remember a specific action that will be required in the future has not been possible and only humans have been tested under such conditions. Also, testing prospective memory for long-term memory in animals has never been done. This experiment will be the first to employ this methodology for testing prospective memory (of episodic nature) in non-human animals and therefore understand if this ability is uniquely human or is also present in other animal species.

The main objective of the second study in the present thesis was, first to extend our understanding of memory for own actions in mammalian taxa to an avian model, hence an extremely distantly related taxon. Secondly, to examine the parrots' concept learning ability and thirdly to compare their performance directly with that of dolphins and pinnipeds in the third and last study of this thesis. In order to gain deeper insights into the phylogenetic distribution of the ability to recall self-performed actions, it is necessary to broaden the comparison to species outside of the mammalian clade. Parrots, a diverse avian order, appear an interesting first model group for investigating memory for own actions because together with dolphins, primates and corvids they stand out among vertebrates in terms of both their relative brain size (M. L. Lambert et al., 2019) and neuron density (N. J. Emery, 2006; Olkowicz et al., 2016) and are considered on a par with great apes in terms of complex cognition (M. L. Lambert et al., 2019). Parrots exhibit high social complexity and long-term monogamy (N. J. Emery & Clayton, 2005b) and share several socio-ecological and cognitive traits with dolphins and primates (Baciadonna et al., 2021; Bradbury & Balsby, 2016; Osvath et al., 2014). However, to date, there are no studies on parrot memory, e.g., for social interactions and third-party relationships, although it seems equally adaptive for them than it has been suggested to be for corvids (Boeckle & Bugnyar, 2012; Marzluff et al., 2010; Taylor, 2014). For instance, in order to show appropriate social behavior, individuals may have to remember specific social events (in terms of what happened where and when and who was involved) that could lead to, for example, sudden changes in the hierarchy. According to Clayton and colleagues (2000) monitoring the interactions of conspecifics and remembering specific social events is crucial for an updated knowledge of the relationships and social dynamics between one’s group members, and the type of memory necessary to perform these functions fits the behavioral criteria of episodic memory. Such a memory of social interactions would of course also include events of one’s own interactions with conspecifics. One example is a study by Emery and Clayton (N. J. Emery & Clayton, 2001) conducted with scrub-jays, where one group of birds experienced stealing other birds’ caches, whereas a second group lacked this experience. Only the group that had experienced being a thief recached their food after having been observed by other individuals (N. J. Emery & Clayton, 2001; Taylor, 2014). If convergent trends in the evolution of sociality and cognition hold, we should therefore see robust memory for one’s own past actions in non-mammalian parrots.

I tested the parrots once they had been trained to perform four different arbitrary behaviours in response to specific hand signals. After that, they were trained to respond reliably to the “repeat command”, i.e., to repeating one out of the four actions they had performed upon command just before, when receiving the command to “repeat”. Test sessions included repeat trials and double repeat trials, where parrots had to repeat immediately after the previously self-performed action, and trials without repeat intermixed as controls, to test if the parrots repeated correctly, only when requested and not relying on a representation of the last behavioral command. To test their memory in self-performed actions, the parrots also received sessions with increasing time delays preceding the repeat command. Extending previous studies, I also tested the parrot’s ability to generalize the repeat rule to novel behaviours. Considering the results from the mammalian studies (Fugazza et al., 2020; Mercado III et al., 1999; Paukner et al., 2007; Scagel & Mercado III, 2022; Smeele et al., 2019) and given that parrots share similar socio-ecological environments (Auersperg & von Bayern, 2019; Baciadonna et al., 2021) and comparable cognitive abilities (Auersperg et al., 2014; Auersperg & von Bayern, 2019; Brucks & von Bayern, 2020; Krasheninnikova et al., 2018; Tassin de Montaigu et al., 2020), I hypothesized that the macaws would be able to learn the abstract rule of repeating their own previous action, to remember self-performed behaviour for delays comparable to those achieved by the mammals tested before, and to transfer the repeat command to novel actions.

Lastly, in the third study, I tested bottlenose dolphins using the same procedure as in Study 2, to directly compare the performance of the dolphins with the previously tested parrots. This procedure was already used in a published study by Smeele et al (2019) with three species of pinnipeds. I trained and collected data in a similar manner with the birds and dolphins in order to compare the results between all five species. The performance for single repeat trials among all tested species by previous studies turned out to be comparable. When testing their memory for actions, i.e., requesting the subjects to perform their last action following a delay, the different studies reported big differences between the species. Dogs were able to remember their own actions for time delays up to one hour (Fugazza et al., 2020), albeit in a so-called unexpected retrieval test, which differed greatly from the experimental procedure of Mercado and colleagues (1998) original study. The dolphins in that study remembered their last action still after two minutes but no longer than that (Mercado et al., 1998), whereas macaques and pinnipeds performed above chance only after 12-30 seconds (Paukner et al., 2007; Smeele et al., 2019).

Given that the results of the previous studies employing the repeat paradigm were not directly comparable, I trained three bottlenose dolphins (*Tursiops truncatus*) on the repeat command following the same experimental procedure with our previous parrot study, and at the same time nearly identical also to the procedure previously used in pinnipeds (differing only slightly in terms of numbers per session but employing the same basic methodology).Our objective was to obtain a first directly comparable data of their set of performance of different comparably social and relatively large-brained animal groups using the same methodology and testing procedure.

In order to achieve a better understanding of the evolution of cognitive traits, in this case, memory for self-performed actions, directly comparative studies in distantly related taxa are necessary (Osvath et al., 2014). The building block of self-representation could be more widespread than the more complex knowledge about the self, or autonoetic consciousness. Our present study comprises the largest comparative data set for memory for self-performed actions by testing a total of 14 individuals from five different species.

In conclusion, the experiments presented in this thesis aim to employ novel methodologies for testing prospective memory in non-human animals and also apply such techniques to studying episodic-like memory, both in dolphins and parrots.

“We are the memory we have

and the responsibility we assume,

without memory we do not exist

and without responsibility

we may not deserve to exist”

Jose Saramago

Materials and Methods

Materials and Methods

Ethical statement

All applicable international, national and/or institutional guidelines for the care and use of animals were followed. The animals from Dolphin Adventure were kept and trained under permits from Mexican Secretariat of Environment and Natural Resources [permit: INE/CITES/DGVS-EF-P-0033-NAY/00 (PIMVS)]. In accordance with the German Animal Welfare Act of 25th May 1998, Section V, Article 7 and the Spanish Animal Welfare Act 32/2007 of 7th November 2007, Preliminary Title, Article 3, the study was classified as non-animal experiment and did not require any approval from a relevant body.

All subjects from all facilities participated in the experiment on a voluntary basis. The dolphins and parrots could choose to come to the experimenter or leave the session and all the food would be given anyway.

Subjects and housing conditions

For the first study, Study 1, on dolphin long-term memory for own actions, data was collected in four females and one male bottlenose dolphins (*Tursiops truncatus*). All dolphins were kept at Dolphin Adventure (Vallarta Adventures) in the west coast of Mexico. The four females, Karina, Eva, Nouba and Lluvia, were 30, 10, 19 and 14 years old, respectively. Eva and Lluvia were sisters. All four females were housed together with 12 more dolphins in a 4 m deep pool system of 2465 m^2 (see Figure 4 for further dimensions). Eva was pregnant and Nouba had a lactating calf during the experiment. Karina was wild-born, whereas Eva, Nouba and Lluvia were born under human care in this facility. The male, Nemo, was 15 years old and was captive-born in this facility. Nemo was housed in a different pool system (1373 m^2; 4 m deep; See Figure 5) together with six other dolphins. All animals had been trained by specialist dolphin trainers on a variety of behaviours performed upon command and displayed for visitors to the facility for multiple years. They received their full diet distributed across the training sessions, independent of their performance. Food was only given during training sessions throughout the day. All subjects were tested individually, but in their home pool while the rest of the group was engaged in their respective training sessions with other trainers in other locations of the same pool at some distance. Testing them alone in a separate pool was not possible, because dolphins are very social animals and separation from their group would have produced stress and a decrease in their attention likely to influence their memorizing performance.

Figure 4. *Aerial view of the dolphin enclosure at Dolphin Adventure where the four females, Karina, Eva, Nouba and Lluvia were housed together with 12 other dolphins. This facility is inland built with concrete pools.*

Figure 5. *Aerial view of the dolphin enclosure at Dolphin Adventure where the male, Nemo was housed together with six other dolphins. This facility is in the harbour and the pool walls are made of sailcloth.*

For all the other studies, I worked with three bottlenose dolphins (*Tursiops truncatus*) and three blue-throated macaws (*Ara glaucogularis)* housed in Loro Parque: Animal Embassy, Tenerife (Spain) (Figure 6). The details on age and sex of the individuals are specified in Table 1. The bottlenose dolphins at Loro Parque were also used as controls for Study 1. The three dolphins, Achille, Ulisse, and Clara were housed in a pool system with interconnected pools between which the animals rotated every day. During training and the test, Achille and Ulisse stayed together whereas Clara was in a separate pool as she had a one-year-old calf with her. All dolphins had been born under human care. All pools were outdoors and exposed to natural weather and light conditions.

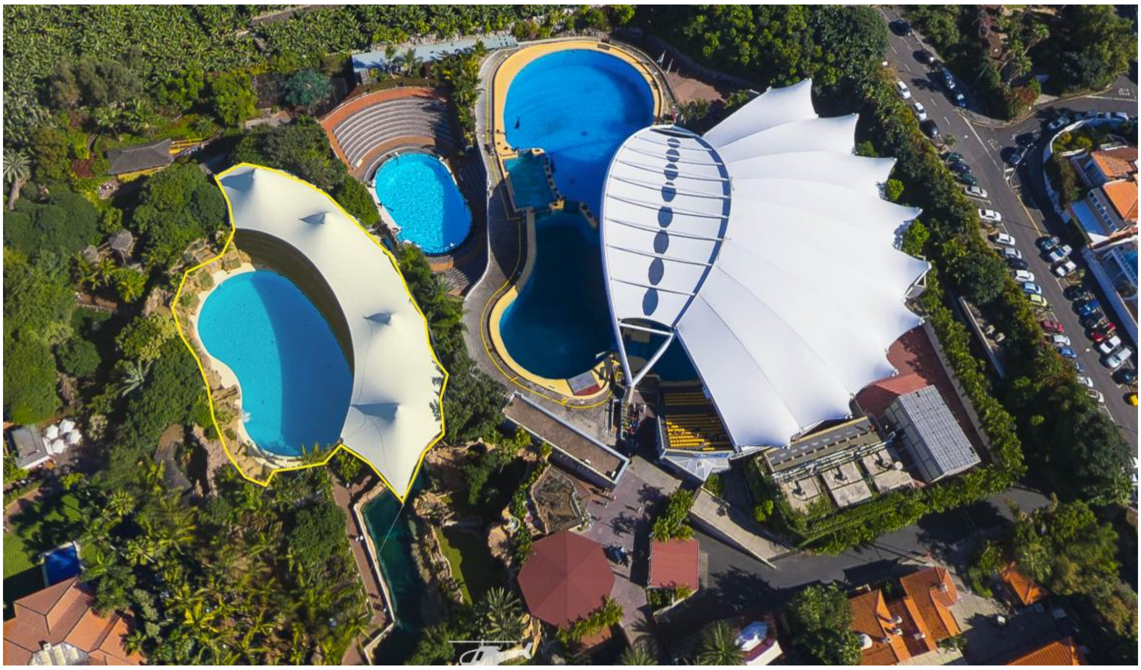


Figure 6. *Aerial view of the dolphin enclosure at Loro Parque: Animal Embassy. The facility housed the dolphins for Study 3. This facility is built inland with concrete pools.*

The dolphins had 4-5 training sessions a day and were fed with a variety of fish (e.g., a mix of herring, sprat, capelin, and blue whiting). All dolphins participated voluntarily both in the training sessions and the experimental sessions. Food deprivation was never used to increase motivation in the animals. During training, all available fish species were used as rewards. Yet, during the testing sessions, only sprat was used so as not to influence the dolphins' response with varying reinforcement. The dolphins were both trained and tested in their pools while the other individuals were trained by one of their caretakers.

Table 1. *Details of the dolphins tested for the experiment.*

Animal ID	Species	Date of birth	Gender
Clara	*Tursiops truncatus*	07/12/1999	Female
Ulisse	*Tursiops truncatus*	03/09/1997	Male
Achille	*Tursiops truncatus*	22/08/2002	Male

Regarding the parrots (Table 2), they were housed in the Comparative Cognition Research Station, inside Loro Parque zoo, in Tenerife (Spain). Loro Parque Foundation staff hand-raised and group-reared all the parrots used in this study. Water was provided ad libitum and the parrots were fed twice a day. All parrots participated voluntarily both in the training sessions and the experimental sessions. During training, sunflower seeds were used as rewards, whereas during testing small pieces of walnut were used.

The parrots were housed in groups of six to eight conspecifics in two different aviaries (1.8 × 3.4 × 3 m each) interconnected by 1 × 1 m windows, which could be closed for separating individuals for testing. Half of the aviary was outdoors so the birds were exposed to natural weather conditions. The other half was covered and lit with Arcadia Zoo Bars (Arcadia 54W freshwater Pro and Arcadia 54W D3 Reptile Lamp) that followed the natural daylight regime.

Table 2. Description of the subjects

Animal ID	Species	Year of Hatching	Gender
Charlie	*Ara glaucogularis*	2014	Male
Mr Huang	*Ara glaucogularis*	2013	Male
Gargamel	*Ara glaucogularis*	2012	Male

A large variety of fruit and vegetables was given both in the morning and in the afternoon. Parrots also received Versele Laga Ara seed-mix portioned according to individual body weight together with the fruit in the afternoon.

Study 1: Long-term memory for own actions in dolphins

Previous behavioural training and selected trained behaviours

The five test dolphins and the two control dolphins were trained using operant conditioning with positive reinforcement (Pryor, 1986; Schapiro et al., 2003). This technique implies giving the animals commands consisting of specific hand gestures, or signals, and when the animal performs the correct behaviour, the trainer will blow a whistle, indicating the dolphin that the behaviour is correct and then reinforce with fish. If the dolphin's response is incorrect, the trainer will not blow the whistle but give a 3-5 seconds break to indicate that the behaviour is incorrect.

For the test dolphins, six behaviours from each dolphin's repertoire of previously trained behaviours were chosen for the experiment. For the control dolphins, four behaviours from their natural repertoires were chosen. We selected behaviours that were assessed to have high energetic cost and that were observed being practiced relatively often (i.e., the chosen behaviours had been learned by the dolphin during several years; Table 3). After phase 1, Karina did "go down" instead of "splash" due to mouth injuries.

Table 3. Description of the previously trained arbitrary behaviours that were used for all experimental conditions and list of which dolphins performed which behaviours.

Behaviour	Description	Animals
Clap	Dolphin in vertical position with head and pectoral flippers out of the water will move its pectoral flippers back and forward rapidly	Test: Karina, Nemo, Nouba, Lluvia, Eva Control: Achille, Ulisse

Spin	Dolphin in vertical position with head out of the water will turn around itself	Test: Karina, Nemo, Nouba, Lluvia, Eva Control: Achille, Ulisse
Tail wave	Dolphin in vertical position but upside down with tail out of the water will move the tail back and forward repeatedly	Test: Karina, Nemo, Nouba, Lluvia, Eva Control: Achille, Ulisse
Jump	Dolphin will jump out of the water with its entire body	Test: Karina, Nemo, Nouba, Lluvia, Eva
Splash	Dolphin in vertical position with head out of the water will squirt/spit water out of its mouth	Test: Karina (only phase 1), Nemo, Nouba, Lluvia, Eva
Sing	Dolphin in vertical position with head out of the water will produce vocalizations	Test: Karina, Nemo, Nouba, Lluvia, Eva
go down	Dolphin sinks to the bottom of the pool until it lies there horizontally on its belly	Test: Karina
belly up	Dolphin will turn their body upside down with their belly facing the water surface	Control: Achille, Ulisse

Specific training for the prospective memory study

a) Training "Memorize and Recall commands"

The commands that instructed the dolphins to memorize a particular behaviour and to recall it in the future were established as described below (Table 4).

Table 4. Description of the behaviours trained for the memory and sequence experiments.

Behaviour	Description	Hand gesture used
Memorize	Command used to let the dolphin know that it should memorize the behaviour following this command	Both index fingers pointing at the dolphin
Go	Command used to let the dolphin know that he can proceed to perform the behaviours that the trainer requested to memorize	Both fists hitting vertically
Sequence	Command used to let the dolphin know that there would be a sequence of behaviours	Both fists in the middle and moving horizontally to each side
Wait	Command used to introduce more than one behaviour in a sequence and letting the dolphin know that it should wait to perform the sequence	Both hands open with the palm facing the dolphin

Reverse	Command used to tell the dolphin to reverse the order of the previously performed sequence of behaviours	Both hands cross in the middle from one side to the opposite side

To memorize a particular previously trained behaviour, the dolphins learned a series of commands containing three different hand signals (*memorize* + *behaviour to be memorized* + *go*), i.e., the "MEMORIZE command". After this instruction, we asked the dolphins to remember and perform the memorized behaviour ("RECALL command"). The chain of commands contained only two hand signals (*memorize* + *go*). After the *go* command, the dolphin had to perform the behaviour that it had been told to memorize even though the *behaviour to be remembered* hand signal was not presented. The dolphin's instruction followed a stereotyped procedure ensuring that the dolphin had actually paid attention to the "MEMORIZE command" and indeed memorized the respective behaviour for later performance. Therefore, straight after the "MEMORIZE command" had been given, the "RECALL command" followed to test whether the dolphin could perform the behaviour instantly. In order to consolidate the memory even more, this procedure, i.e. the "RECALL command" was repeated twice more, following an interval of e.g., 1min and 3min respectively (= one- and three-minute checks). If the dolphin could perform the behaviour each time, the real trial started with the respective delay followed by the recall test (i.e., the "RECALL command"). For the trials where the procedure was restarted, the "MEMORIZE command" was used instead of the recall command (Figure 7).

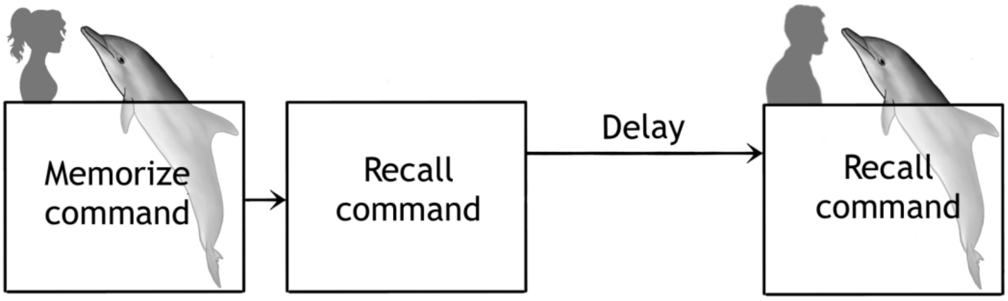


Figure 7. *Illustration representing the procedure of each experimental trial.*

In order to train the “MEMORIZE command”, we first introduced the hand signal “memorize” (Table 4) and reinforced the animal for paying attention to the trainer. After this, we introduced a robust behaviour from their repertoire (a highly reinforced behaviour that the subject has known for years), i.e., giving the command for carrying out that specific behaviour after the “memorize signal”. Yet, we immediately prevented the dolphin from performing that behaviour straight away so that it learned that when a behaviour command was given following the “memorize” signal, it should not perform the behaviour immediately after the hand signal but wait for a while. Once the dolphin was able not perform the behaviour straight after the “*memorize*” + “*behaviour*” signal, the “*go*” signal was introduced and the dolphin learned to perform the behaviour only after the “go” signal was given. When the dolphin waited until the “go” signal to perform the specific requested behaviour reliably, i.e., when it had learned the full signal series (“memorize” + behaviour + “go”), the trainer started introducing the “RECALL command”, i.e., the “memorize” and “go” signal without specifying the behaviour again (which we named as “RECALL” command), straight after the “MEMORIZE command” and thus requested the dolphin to perform the previous behaviour again.

After successful learning of the “RECALL command” and establishing the repetitions of the “RECALL command” after each “MEMORIZE command” (see Figure 7), the delay in between the memorization of the behaviour and the recall was gradually introduced. First, the time between the last “RECALL command” (as part of the memorization) and the actual “RECALL command” was increased in small steps until 15-30 seconds delay was reached for each participating dolphin. Then, intermediate behaviours were introduced, i.e., the dolphins performed other behaviours during the delay phase before receiving the final “RECALL command”. The trainers started with simple incompatible behaviours, like e.g., swim around. An incompatible behaviour was a behaviour that the dolphin could not perform simultaneously with the memorized behaviour. Finally, the trainer introduced more behaviours, also including compatible ones during the delay. Lastly, the trainer followed the same training process but introduced new behaviours selected to be memorized during the experiment (Table 3).

Each dolphin was trained with each six behaviours employed until a delay of 1 hour was reached. The training of the “MEMORIZE” and “RECALL commands” for the experiment started on 22 April 2020. Testing started when dolphins reached a criterion of 10 correct trials from a total of 18 trials (55% correct) with a delay of 15 minutes without distractions.

b) Training of the control group

Two dolphins constituted the control group. The training of the control group started the 16th of May 2022 (Table 5). The training steps were the same as for the testing group, except that the control dolphins were tested without training them for incremental delays of time between memorizing and recalling an action. For 20 days, the dolphins were trained in the “MEMORIZE” and “RECALL” commands without time delays exceeding 3min in between or intermediate behaviours. Then from the 9th of June, the trainers started to introduce distractive actions between the memorization of the action and the recall of the action that the dolphin had to memorize. The delays between memorization and recall were never longer than three minutes. Data collection with the control dolphins started the 15th of June of 2022 (Table 5).

c) Training of the "Sequence command"

After the five test dolphins had learned consistently to memorize different behaviours, they were trained for the concept of "behavioural sequence". To train this behaviour, a hand signal that meant "Sequence" was introduced. Initially, the trainer reinforced the dolphin for just paying attention to it. Subsequently, he showed it followed by a simple "on situ" behaviour from their repertoire (i.e., a behaviour performed at the site, rather than a jump or something that would require the dolphin to swim away) but immediately stopped the dolphin from performing the behaviour in order to make it wait for the "go" hand signal first. Once the dolphin was able to abstain from performing the behaviour after the *"sequence"* + *"behaviour"* signal, the "go" signal was introduced and the dolphin was allowed to perform the behaviour (Table 4). When the dolphin reliably waited until the "go" signal before performing the specific behaviour, the trainer introduced a "wait" signal after the first behaviour and added a second behaviour. Trainers would help the dolphins to learn that after the "go" signal, they needed to perform two behaviours, by giving them the commands (e.g., clap and spin, sing and clap). The help from the trainers would then be faded away slowly by helping only in some trials, or helping only with one of the behaviours of the sequence.

The chain of hand signals presented to the dolphins to memorize a sequence were: "*memorize*" + "*sequence*" + "*behaviour 1*" + "*wait*" + "*behaviour 2*" + "*wait*" + "*behaviour 3*" + "*go*". The "SEQUENCE command" had been trained previously in 2012-2013. We assumed the dolphins understood the concept of sequence when they reached the criterion of performing 10 correct trials from a total of 18 trials (55% correct) of sequences without delay. Testing to remember sequences started without training them to remember sequences.

d) Training of the “Reverse sequence command”

In the last part of the study, a test group dolphin was required to reverse the sequence of two behaviours. This was trained by implementing a new hand signal that meant “*reverse*” right after the dolphin had performed a sequence. Initially, the trainer “helped” the dolphin by instructing them on which behaviours to do one by one, and after some practice, this “help” was gradually faded out, until none was required, and the dolphins reliably reversed the order of two behaviours upon command.

The “REVERSE command” was previously trained during the years 2016-2017. Testing occurred once dolphins reached the criterion of performing 10 correct trials from a total of 18 trials (55% correct) of reversing a sequence without delay. Testing started on 22 June 2020, and one or two trials a day were conducted, separated by at least two hours. All training and testing session varied in location and time of the day daily. The experiment ended on 2nd March 2021.

Table 5. *Details of the time frame when the study took place with each individual.*

Individual	Group	Experiment	Type	Start date	End date
Nemo	Test	Exp. 1: single behaviour	Training	22/04/2020	21/06/2020
		Exp. 1: single behaviour	Testing	22/06/2020	21/10/2020
		Exp. 2a: sequence of two	Training	2012 - 2013	-
		Exp. 2a: sequence of two	Testing	23/10/2020	26/11/2020
		Exp. 2b: sequence of three	Training	2012 - 2013	-

		Exp. 2b: sequence of three	Testing	01/01/2021	28/01/2021
		Exp. 3: reverse	Training	2016 - 2017	-
		Exp. 3: reverse	Testing	22/02/2021	02/03/2021
Karina	Test	Exp. 1: single behaviour	Training	22/04/2020	21/06/2020
		Exp. 1: single behaviour	Testing	22/06/2020	02/11/2020
		Exp. 2a: sequence of two	Training	2012 - 2013	-
		Exp. 2a: sequence of two	Testing	15/11/2020	21/12/2020
		Exp. 2b: sequence of three	Training	2012 - 2013	-
		Exp. 2b: sequence of three	Testing	28/12/2020	26/01/2021
		Exp. 3: reverse	Training	2016 - 2017	-
Eva	Test	Exp. 1: single behaviour	Training	22/04/2020	21/06/2020
		Exp. 1: single behaviour	Testing	22/06/2020	22/10/2020
Nouba	Test	Exp. 1: single behaviour	Training	22/04/2020	21/06/2020
		Exp. 1: single behaviour	Testing	22/06/2020	15/10/2020
Lluvia	Test	Exp. 1: single behaviour	Training	22/04/2020	21/06/2020
		Exp. 1: single behaviour	Testing	22/06/2020	28/10/2020
Achille	Control	Exp. 1: single behaviour	Training	16/05/2022	14/06/2022
		Exp. 1: single behaviour	Testing	15/06/2022	27/08/2022
		Exp. 4: commands	Testing	29/09/2022	14/10/2022
Ulisse	Control	Exp. 1: single behaviour	Training	16/05/2022	14/06/2022
		Exp. 1: single behaviour	Testing	15/06/2022	18/09/2022
		Exp. 4: commands	Testing	29/09/2022	14/10/2022

Experimental procedures

The prospective memory study consisted of three experiments: 1) prospective memory of a single memorized behaviour, 2) prospective memory of a sequence of up to three memorized behaviours and 3) reversing sequence of two behaviours.

Experiment 1: Memory of a single behaviour

In the first experiment, after having reached the training criterion (10 correct trials out of a total of 18 trials), all five test dolphins were instructed to memorize one of six chosen behaviours out of their respective behavioural repertoire (see Table 3) and requested to recall it after time delays ranging from 0 min to 16 hours. For the control dolphins, they were also instructed to memorize one of four chosen behaviour but requested to recall it directly after a delay of two hours. If a dolphin performed the correct behaviour it had been asked to memorize, then the trainer would let it know that the response was correct by blowing a whistle, and right after, reinforcement in the form of fish would be provided. If they displayed an incorrect or no behaviour the trainer would apply what is called Least Reinforcement Scenario, where the trainer would maintain a neutral position in front of the dolphin and wait for 3-5 seconds, during which the dolphin is just waiting, paying attention to the trainer. The neutral position would show to the dolphin the lack of reinforcement and was used to let the animal know that the response was incorrect. The trial is then counted as incorrect, and a new trial will start later on with the next command from the randomized list.

The experiment for the test dolphins was divided into seven phases and a baseline. The control dolphins had one phase, a baseline and unexpected trial after 16-17 hours delay. The baseline consisted of 18 trials in which the "RECALL command" was given straight after the "MEMORIZE command", i.e., without an intermediate time delay (= No delay baseline trials). The baseline was collected to account for mistakes occurring naturally due to a lack of attention or due to parameters outside our control. For the remaining seven phases, each had a specific delay before the “RECALL command” was given and the behaviour had to be remembered (Table 2). A trial started with the “MEMORIZE command” and the behaviour to be memorized and ended when the dolphin had displayed the behaviour upon “RECALL command” following the time delay for the required phase (Table 5).

Each phase consisted of 18 trials featuring one of the six behaviours in pseudorandom order and counter-balanced, including a minimum of ten double-blind trials (At least 55% of the 18 trials). The number of double-blind trials depended on personal availability. For each trial, all trainers wore sunglasses that prevented the dolphins from seeing the trainers’ eyes and they were instructed to keep their body still in order to prevent any unintended cueing. In the double-blind trials, the trainer who asked the dolphin to recall the behaviour after the delay was another person than the trainer who asked the dolphin to memorize the behaviour at the beginning of the trial. This ensured the trainer giving the “RECALL command” was naïve with respect to the behaviours, which the dolphin was supposed to remember and therefore could not inadvertently cue the dolphin to respond correctly (Sebeok & Rosenthal, 1981).

In order to judge how distraction (see definition below) during the delay interval between the “MEMORIZE” and “RECALL command” would affect their performance, it was tested after the same time delay with and without distraction. In the trials without distraction, the dolphin was instructed to memorize a behaviour and, after a predetermined period of time, during which the dolphin could swim freely but did not interact with any human trainer, the dolphin was called by the trainer and instructed to recall the behaviour. In contrast, in the trials with distraction, the dolphin was instructed to memorize a behaviour and during the predetermined delay, the dolphin would engage in different activities with human trainers (and move freely in the pool with the other dolphins). The trainer would simply continue with a characteristic training session, more training session(s) with the same or different trainers would take place, a medical procedure would be carried out (i.e., blood sample, ultrasound session), or the dolphin would take part in one of the dolphin interactive swimming programs of the facility.

After the predetermined time, the dolphin was instructed to recall the behaviour. The delay ranged up to 16 hours. Due to time constraints of the study, we did not test the dolphins after even longer delays.

Table 5. Experimental phases of the prospective memory experiment regarding single memorized behaviours and their descriptions for the test dolphins. The control dolphins were only tested for the baseline and directly for phase #3, and a single unexpected trial similar to phase #6.

Phase #	**Delay**	**Distractions**	**Description**
1	~ 15 min	No	MEMORIZE at the beginning of a training session and RECALL at the end
2	~ 15 min	Yes	MEMORIZE at the beginning of a training session and RECALL at the end
3	~ 2 hours	No	MEMORIZE at the end of a training session and RECALL at the beginning of the next training session
4	~ 2 hours	Yes	MEMORIZE at the beginning of a training session and RECALL at the beginning of the next training session
5	~ 4 hours	Yes	MEMORIZE at the beginning of a training session and RECALL at the end of the next training session

6	~ 16 hours	No	MEMORIZE at the end of the last training session of the day and RECALL at the beginning of the first training session the following day (= overnight)
7	~ 6 hours	Yes	MEMORIZE at the beginning of the first training session of the day and RECALL at the beginning of the final training session at the end of the day

Experiment 2 a) Memory of a sequence of two behaviours

Two dolphins participated in this experiment: Nemo and Karina. Four of the previously trained behaviours were chosen for the sequence test trials (jump, sing, spin, and tail wave; see Table 3). The experiment was divided into three phases and a baseline without delay (see description above). Each of the remaining three phases had a specific delay before the “RECALL command” (Table 6). A trial started with the “MEMORIZE command” and ended when the dolphin had displayed a behaviour after the delay following the “RECALL command”.

Each phase had 18 double-blind trials and it was pseudorandomized and counterbalanced as regards which behaviours were to be memorized and in which order. Due to time constraints of the study, two hours were the maximum delay tested to investigate the dolphins’ ability to remember sequences of two behaviours.

Table 6. Number of experimental phases of the prospective memory experiment using sequences of two behaviours, and their descriptions.

Phase #	Delay	Distractions	Description
1	~ 5 min	Yes	MEMORIZE at the beginning of a training session and RECALL at the end
2	~ 15 min	Yes	MEMORIZE at the beginning of a training session and RECALL at the end
3	~ 2 hours	Yes	MEMORIZE at the beginning of a training session and RECALL at the beginning of the next training session

Experiment 2b) Memory of a sequence of three behaviours

The same two dolphins as in experiment 2a) participated in this experiment: Nemo and Karina. The same four behaviours were chosen for the sequence test trials (jump, sing, spin, and tail wave; see Table 3). The experiment had only a single phase of 15 minutes and a baseline. For the test phase, a trial started with the "MEMORIZE command" and ended when the dolphin had displayed a behaviour within 15 min following the "RECALL command". This phase consisted of 18 double-blind trials and it was pseudorandomized and counterbalanced regarding which behaviours were to be memorized and in which order. Due to time constraints of the study, the dolphins' prospective memory performance could be tested with a delay of 15 minutes only.

Experiment 3: Reversal of a sequence of two behaviours

Nemo and Karina were trained for the reversal of sequences but only Nemo was tested because Karina gave birth after two testing sessions, and her attention decreased continuously during this period. The same four behaviours as in the previous experiments were used (jump, sing, spin and tail wave; see Table 3). This experiment had only the no delay baseline condition, which consisted of 16 trials without intermediate time delay.

Experiment 3: Memory for commands

The control dolphins were then tested for their memory for the trainer's hand command indicating the behaviour, i.e. without letting the dolphins self-perform the behaviour. For this experiment, the "MEMORIZE command" was implemented in the following manner: ("memorize" + behaviour + delay + "go"). The two dolphins were testing in two conditions: a short-term memory condition with a delay of 10 seconds, and a long-term memory condition with a delay of 60 seconds. Each condition had 8 trials with 4 randomized and counterbalanced actions.

Data analysis

All analyses were performed using the *rethinking* (McElreath, 2020) package in R (R. C. Team, 2013).

No delay baseline trials

To test how well animals performed without any delay, we estimated the overall probability of the dolphins showing the memorized behaviour correctly. We used a Bayesian logistic model with varying intercepts for animal and behaviour:

$$
\begin{aligned}
\text{response}_i &\sim \text{binomial}(1, p_i)\\
\text{logit}(p_i) &= \alpha_{\text{individual}[i]} + \gamma_{\text{behaviour}[i]}\\
\alpha &\sim \text{normal}(\overline{\alpha}, \sigma_\alpha)\\
\gamma &\sim \text{normal}(0, \sigma_\gamma)\\
\overline{\alpha} &\sim \text{normal}(0,1)\\
\sigma_\alpha &\sim \text{exponential}(1)\\
\sigma_\gamma &\sim \text{exponential}(1).
\end{aligned}
$$

The response (correct, incorrect) was modelled using a binomial distribution. We used a logit transform for the probability that the ith observation was correct (p_i). The model contained an average performance ($\overline{\alpha}$), an off-set (varying effect) per individual (α) and per behaviour (γ). The two σ parameters control the strength of each varying effect. We choose slightly regularising priors that limited the model to sensible values. Normal(0, 1) translates to most values on the probability scale between 11-89% and exponential(1) translates to mass centred around σ = 1.

We assumed the probability of the animal responding with the correct behaviour was 1/6 if the animal performance was at random. This is a conservative estimate, because the animal could also respond with a behaviour not part of the six behaviours in the test set.

The effect of recall latency and distraction during the delay

Since the experiment was conducted in discrete phases, with each phase representing a discrete increase in difficulty, we treated the phase as an ordered categorical variable. We used a similar Bayesian logistic model, including animal, behaviour, double blind, date, and had the "MEMORIZE command" for the behaviour and "RECALL command" for the behaviour as varying effects on the intercept. We also included the normalized natural logarithm of the number of distractions and the phase as predictors. We included varying effects for animals on the slopes to allow individuals to respond differently to these challenges.

$$
\begin{aligned}
\text{response}_i &\sim \text{binomial}(1, p_i) \\
\text{logit}(p_i) &= \phi_i - \beta_{\text{I}[i]} * \sum_{j=0}^{\text{P}[i]-1} \delta_j + \xi_{\text{I}[i]} * \text{LD}_{[i]} \\
\phi_i &= \alpha_{\text{I}[i]} + \gamma_{\text{B}[i]} + \zeta_{\text{DB}[i]} + \eta_{\text{D}[i]} + \iota_{\text{TM}[i]} + \kappa_{\text{TR}[i]} \\
\alpha &\sim \text{normal}(\overline{\alpha}, \sigma_\alpha) \\
\overline{\alpha} &\sim \text{normal}(0,1) \\
\gamma &\sim \text{normal}(0, \sigma_\gamma) \\
\zeta &\sim \text{normal}(0, \sigma_\zeta) \\
\eta &\sim \text{normal}(0, \sigma_\eta) \\
\iota &\sim \text{normal}(0, \sigma_\iota) \\
\kappa &\sim \text{normal}(0, \sigma_\kappa) \\
\beta &\sim \text{normal}(\overline{\beta}, \sigma_\beta) \\
\overline{\beta} &\sim \text{exponential}(1) \\
\xi &\sim \text{normal}(\overline{\xi}, \sigma_\xi) \\
\overline{\xi} &\sim \text{normal}(0,1) \\
\sigma_{\alpha:\xi} &\sim \text{exponential}(1) \\
\delta &\sim \text{dirichlet}(2).
\end{aligned}
$$

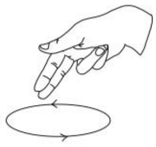
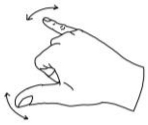
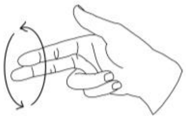
Model structure was similar to the one used for the no delay baseline trials, but also included varying effects for: individual ($\alpha_{\text{I}[i]}$), behaviour ($\gamma_{\text{B}[i]}$), double blind ($\zeta_{\text{DB}[i]}$), date ($\eta_{\text{D}[i]}$), trainer memorize ($\iota_{\text{TM}[i]}$), trainer recall ($\kappa_{\text{TR}[i]}$); and included a varying slope ($\xi_{\text{I}[i]}$) for the effect of normalized log number of distractions (LD). It also included phase as ordinal effect. For this the varying slope ($\beta_{\text{I}[i]}$) for phase was multiplied by the sum of the δ_j's up to j = phase. In this way the δ_j's represent the marginal increase in log-odds that graduating from phase n to m has. Both slopes contained varying effects with respect to individual, allowing individuals to differ in their sensitivity to time and distraction. We restricted the slope of the phase to negative values but allowed positive values for the slope of the distractions.

Study 2: Memory for own actions in parrots

Experimental setup and general procedures

The birds were trained and tested individually in separate testing rooms (1.5 x 1.5 x 1.5 m) artificially lit with daylight lamps (Arcadia Zoo Bars ©), which the birds were well habituated to. During the experiment, the subject sat on a perch facing the experimenter who stood inside the test room on the opposite side wearing mirror-glass but blinded sunglasses. A second person, the assistant, also wore mirrored but see-through sunglasses and observed the experiment through a window from the neighbouring room. The experimenter gave the experimental commands (Table 7) to the parrot but could not see its response. If the parrot responded correctly to the command, the assistant in the neighbouring room gave the parrot a whistle blow as immediate conditioned reinforcer, followed by a food reward (a piece of walnut) as positive reinforcement. If the parrot did not respond correctly, the whistle was not blown, no reward was given and the next trial started following a three second pause. The experimenter gave an equal piece of walnut every time the parrot performed a behaviour. The order of behavioural commands and repeat commands given in each session, was pseudo-randomized and counterbalanced across birds and determined before the session. The assistant also signalled to the experimenter which command to give next by showing the behaviour label on the screen of an iPad visible only for the experimenter.

Table 7. Description of the behaviours trained for the repeat test and the delayed repeat test.

Behaviour	Description	Hand gesture used (=command)	Hand gesture illustrated
Spin	The parrot spins around its own axis in a clockwise direction	The index finger rotates in a circular movement in clockwise direction over the parrot's head	
Wings	The parrot flaps its wings once	Palm of the hand open and extended moving up and down repeatedly	
Lift right leg	The parrot lifts up its right leg	Index finger in vertical position and remaining fingers closed	
Head shake	The parrot shakes its head once	Clenched fist turned horizontally with see-sawing extended thumb and little finger	
Repeat	The parrot repeats the last behaviour it had performed upon behavioural command	Index and middle finger extended horizontally and circling	

Testing criterion

After all animals had been trained for the four actions and the repeat command, the reliability of their response to the repeat command was tested in a 20-trial session, in which the command for one of the four trained behaviours was given either followed by a “repeat” command in 60% of the trials or by a command for one of the four behaviours (remaining 40%). This was implemented to prevent the animal from learning to simply repeat the first command in every trial. The list of commands was randomized and counter-balanced. To reach the criterion, the animal had to perform at least 7 repeats out of 12 (58%) correctly during the session.

Experimental conditions

Repeat test

To test the animals’ ability to repeat their own previous behaviour on command, eight experimental sessions consisting of 26 trials each were completed. A “single repeat” trial was composed of the command for one of the four trained actions followed by the repeat command. A “double repeat” trial started with the command for one of the four trained actions followed by a repeat and a second repeat command (Figure 8A). There was no training for the double repeat trials. The first “repeat” of a “double repeat” trial, was analysed as a “single repeat trial” for the results. The “control” trials consisted of requesting one of the four trained actions, followed by the command for another one of the four trained actions. Four of the trials (15%) were “single repeats”, eight (30%) were “double repeats” and ten trials (38%) were “controls”.

Delayed repeat test

To test for how long the animals could remember their own previous behaviour, gradually increasing delays were introduced between the behaviour and the repeat command. Only single repeat trials (16 trials per session, and 6 sessions) were performed. A staircase paradigm in which a delay increased 3 s after a correct response and decreased 3 s after an incorrect response was implemented (Figure 8B).

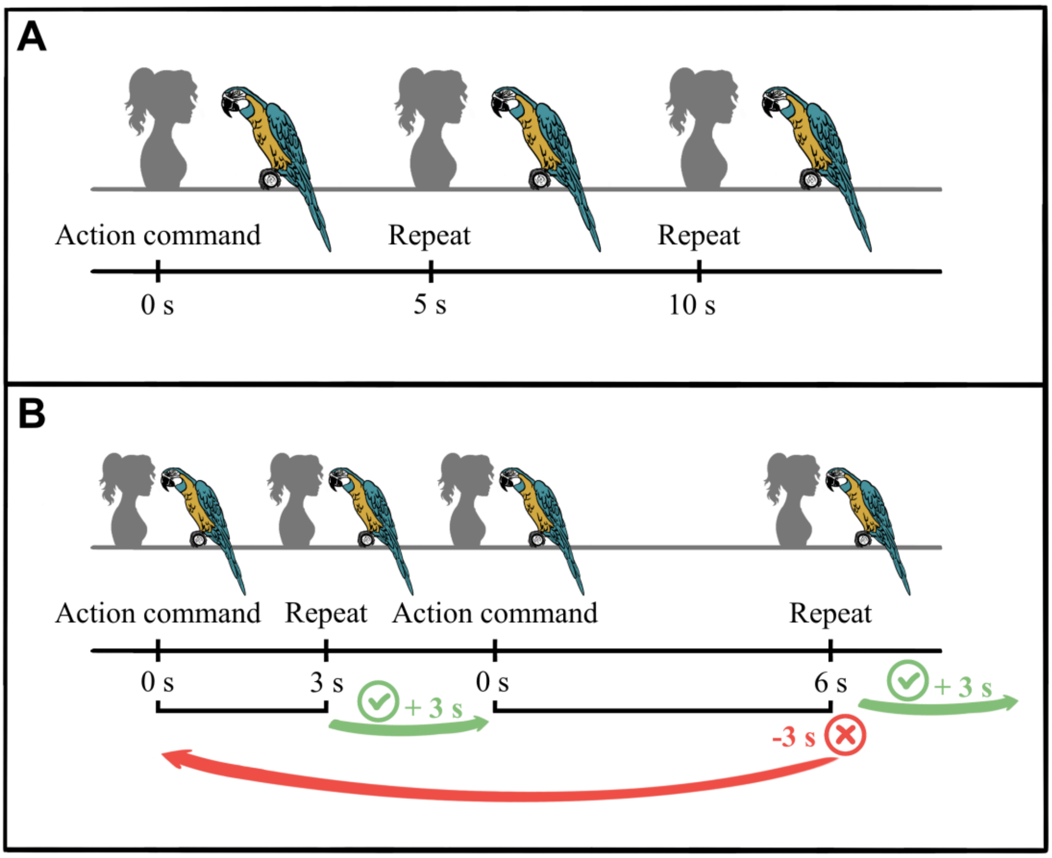


Figure 8. **(A)** Illustration for the double-repeat trial procedure and the delays between the different commands. **(B)** Delayed repeat test procedure. If the parrot repeated correctly, the delay increased three seconds in the next trial, otherwise, the delay decreased three seconds.

For the delay test, the assistant stood next to the experimenter inside the room together with the parrot. The assistant held a computer and communicated the next command to be given verbally to the experimenter. The list of behaviours was imported into an R session (RStudio, version 1.1.383). The R session displayed the next behaviour to be requested to the assistant in the computer screen once the delay had passed. The assistant would then communicate it to the experimenter, after having entered the parrot's response (correct or not). This automatically updated the delay duration for the following trial.

Novel behaviour repeat test

To test if the parrots could generalize the repeat rule and apply it to novel behaviours, i.e., trained behaviours that the parrots display upon a specific gestural command, but that they had never been asked to repeat before, we tested if the parrots were capable of repeating three newly trained behaviours spontaneously from the first repeat trial (Fugazza et al., 2020; Mercado et al., 1998; Pack et al., 1991). The parrots were therefore trained to perform three novel behaviours upon specific commands. Once the parrot performed the behaviour associated with the hand signal reliably, we started the test. The first test session started with a trial in which the subject was requested to perform the new behaviour followed by the repeat command. Subsequently, the experimenter continued for 2-4 more trials with previously known behaviours and then requested the new behaviour again, followed by the repeat command. If the new behaviour was repeated correctly in the first trial and the second trial, the parrot was considered successful. And the training for a new behaviour started the following day.

Repeat command training

First, the parrots needed to be trained to perceive the neutral stimulus of a dog whistle as a conditioning stimulus by pairing it with food rewards (Pryor, 1986). The whistle was required for reinforcing desired behaviours in the right moment followed by administration of sunflower seeds as food reward. The frequency of the desired behaviour increased by gradual shaping. All parrots were first trained to provide attention to the experimenter. After the parrot had learned to perch calmly in front of the experimenter and attend to her, the four actions were trained and associated with the different hand gestures (Table 7).

All subjects were trained using the same training steps:

1. The experimenter requested one of the four trained actions five times in a row by the respective command and then introduced the repeat command expecting the animal to repeat the chosen action by inertia.
2. The experimenter then switched to a different action (than the previous) and requested the parrot to perform it five times. After that, again the repeat command was given. If the animal did not repeat the second action, the experimenter would request the second action paired with the repeat command until successfully performed by the parrot consistently. When the parrot repeated the second behaviour correctly, then the experimenter intermixed action 1 and action 2, asking each action 5 times followed by the repeat command. The number of times each action was asked before the repeat command would then decrease slowly until the animal discriminated correctly and needed only two previous presentations to correctly repeat.
3. After the parrots were able to consistently repeat the two actions on command, the experimenter requested a third action just once and then gave the repeat command to test if the parrots were able to repeat a novel action without training. If the animal failed, then the experimenter requested the third action five times and then gave the repeat command again as in step 1. If the animal repeated successfully, the experimenter requested it to repeat the three learned actions in random order until the animals discriminated the repetition of those three actions reliably. If the animal failed, the experimenter repeated training sessions with the parrot on repeating the third action until it consistently repeated it.

4. Once the animals repeated three actions consistently, the last action was requested followed by the repeat command, to test if the parrots could repeat the fourth "new" behaviour instantly. If the animal failed, the experimenter requested the fourth action five times consecutively and then gave the repeat command as stated in step 1. If the animal repeated correctly, the experimenter repeated the four actions in random order until good discrimination is achieved. If the animal failed, the experimenter performed training sessions until the animal repeated the fourth action consistently.
5. The experimenter repeated training sessions on repeating the four actions until each animal passed the criterion. The criterion consisted in repeating seven times correctly out of 12 repeat trials. The total number of trials was 28 with 16 control trials (with a 0.25% chance level).

Statistical analysis

Performance in the repeat test

To test if individuals could remember their own previous behaviour, we estimated the probability of responding correctly to the repeat command and compared this to chance-level. We assumed the chance-level to be 1/4 if they chose one of the four behaviours randomly or if they showed a preference for one of these behaviour on all trials. To estimate the probability of success we used a Bayesian multilevel model with the following structure:

$$\begin{aligned}
\text{response}_i &\sim \text{binomial}(1,\ p_i) \\
\text{logit}(p_i) &= \alpha_{\text{individual}[i]} + \gamma_{\text{behaviour}[i]} \\
\alpha &\sim \text{normal}(\overline{\alpha},\ \sigma_\alpha) \\
\overline{\alpha} &\sim \text{normal}(-0.5,\ 1) \\
\gamma &\sim \text{normal}(0,\ \sigma_\gamma) \\
\sigma_\alpha &\sim \text{exponential}(1) \\
\sigma_\gamma &\sim \text{exponential}(2)
\end{aligned}$$

The prior for the average performance was chosen to centre most mass around the chance level of 1/4.

To test performance on the double repeat task the same model was used, with the only modification that the prior for alpha_bar was centred around -1. Models were fitted using *ulam* from the *rethinking* package (McElreath, 2020) which runs the Stan sampler using the *cmstanr* interface. We ran four chains with 8000 iterations and a 500-iteration warm-up. Rhat and divergence were monitored.

Performance in the delayed "repeat" test

To test if and how performance declined with increasing delay between the initial behaviour and the repeat command a similar Bayesian model was used with a multilevel slope added:

$$\begin{aligned}
\text{response}_i &\sim \text{binomial}(1,\ p_i)\\
\text{logit}(p_i) &= \alpha_{\text{individual}[i]} + \gamma_{\text{behaviour}[i]} + \beta_{[i]} * \log(\text{time})\\
\alpha &\sim \text{normal}(\overline{\alpha},\ \sigma_\alpha)\\
\overline{\alpha} &\sim \text{normal}(-1,\ 1)\\
\gamma &\sim \text{normal}(0,\ \sigma_\gamma)\\
\beta_{[i]} &= \zeta_{\text{individual}[i]} + \iota_{\text{behaviour}[i]}\\
\zeta &\sim \text{normal}(0,\ \sigma_\zeta)\\
\iota &\sim \text{normal}(0,\ \sigma_\iota)\\
\sigma_\alpha, \sigma_\gamma, \sigma_\zeta, \sigma_\iota &\sim \text{exponential}(2)
\end{aligned}$$

Study 3: Memory for self-performed actions in parrots, dolphins, and pinnipeds: a comparative approach

Training

All dolphins had previous experience with operant conditioning training and exhibited a large repertoire of trained behaviours (i.e., “actions”), which they could execute upon specific commands (i.e., hand and or sound signals). The experimenter chose four trained behaviours that had been established and used on a regular basis for several years and that appeared to require comparable effort/energetic costs (Table 8).

Table 8. *Description of the behaviours used during testing.*

Behaviour	Description
clap	Dolphin in vertical position with head and pectoral flippers out of the water will move its pectoral flippers back and forward rapidly
spin	Dolphin in vertical position with head out of the water will turn around itself
sing	Dolphin in vertical position with head out of the water will produce vocalizations
belly up	Dolphin will turn their body upside down with their belly facing the water surface

Concerning the repeat command, all dolphins were trained using the identical training steps that were implemented in parrots in the Study 2: Episodic content awareness in parrots.

Experimental set up

During testing, one experimenter stood in front of the dolphin wearing mirrored and blinded sunglasses. The experimenter gave the hand signals for the respective requested behaviour to the dolphins but did not see the response. If the dolphin responded correctly to the signal given, an assistant beside the experimenter, also wearing mirrored glass sunglasses (but not blinded) blew a whistle that indicated that the performed behaviour was correct to both the animal and the experimenter. Upon hearing the whistle, the experimenter reinforced the dolphin with food. If the whistle was not used, the response was incorrect, and the experimenter continued with the next trial after a pause of three seconds. The assistant also held an iPad showing the next action to be performed on the screen, visible only for the experimenter.

Repeat paradigm

Repeat testing criterion

After all animals had been trained responding to the “repeat” command, they had to meet the criterion before they could proceed to testing. They were tested in a session consisting of 20 trials with two commands. The first command was always one of the four trained actions, and the second command was either a “repeat” in 60% of the trials (12 trials) or the command for one of the four actions (8 trials). This procedure prevented the animals from learning to repeat the first command on every trial. The list was randomized and counterbalanced. To reach criterion, the dolphin had to perform at least 7 correct repeats out of 12 (58%) during the session. Clara required 50 training sessions, Achille 60 training sessions and Ulisse 75 training sessions before passing criterion. Parrots passed criterion after around 60 training sessions. Regarding the pinnipeds, the sea lions required 60-80 training sessions while both the grey seal and the harbour seals needed 100-150 training sessions.

Repeat test

To examine the dolphins' ability to repeat their own actions, eight experimental sessions were completed after they had passed training criterion. Each session had 26 trials consisting of two commands per trial. Six of the trials were "single repeats" (23%), eight trials were "double repeats" (31%) and 12 trials were "controls" (46%). In "controls" an action was followed by the command for another of the four actions, instead of a repeat. The first response to the first repeat of a double repeat trial, was analysed as a single repeat trial for the results. The double repeat trials were used to examine whether the animals remembered their own behaviour or the last given command by the experimenter. None of the five tested subjects had received training for the double repeat trials.

Delayed repeat test

To test for how long the dolphins could remember their own previous action, delays were introduced between the last action carried out upon command and the repeat command and also between control trials. The first trial was with a three second delay and then a staircase paradigm was used in which delays increased by three seconds after a correct response and decreased by three seconds after an incorrect response. With this method we aimed to determine the animals' memory limit.

The list of behaviours was imported into an R-script (the statistical programme RStudio, version 1.1.383 (Rs. Team, 2021)). The script displayed the next command to be given to the assistant after the delay. The assistant entered if the response was correct or not, so that the delay for the following trial was automatically adjusted. For the delayed repeat test, the assistant had a computer and communicated to the experimenter verbally which command to give to the dolphin. For all five subjects the delayed repeat test followed on straight after the repeat test without training.

Novel behaviour repeat test

After the general training and test phase with four different behavioural commands, we aimed at examining how much exposure to new (i.e., not yet repeated) behaviours the dolphins required, before they could generalise the "repeat rule" to new behaviours spontaneously and without previous training. The chosen behaviours were known by animals for years but they had never been asked to repeat them. We therefore run test sessions into which such "novel" behaviours were integrated and asked the dolphins to repeat them without previous training, thus testing their ability to "repeat" on first exposure. If a dolphin failed at first trial, we continued repeat training as for the original four behaviours, until they were able to repeat at the beginning of a session and intermixed with previously learned behaviours, before starting with the next "novel behaviour repeat test". A novel repeat test was considered successful when the dolphin repeated the novel behaviour at the beginning of the session at first trial, and then also correctly when intermixed with previously learned behaviours. We assumed the "repeat rule" was understood when the animals spontaneously repeated two novel behaviours when they received the repeat command after the respective behavioural command.

Comparative data on parrots and pinnipeds

To compare the repeat performance of five different animal species including the dolphin tested for this study, raw data were obtained from two previously published studies that used directly comparable methods. Parrot data (blue-throated macaws, *Ara glaucogularis*) was acquired from the second study in this thesis (Study 2: episodic content awareness in parrots). For pinnipeds, the data was acquired from (Smeele et al., 2019). The number of individuals tested were three blue-throated macaws (*Ara glaucogularis*), one grey seal (*Halichoerus grypus*), two harbour seals (*Phoca vitulina*) and five Patagonian sea lions (*Otaria flavescens*).

Statistical analysis

Performance in the repeat test

Previous work had shown that all species could perform the single and double repeat test well above chance-level. In the current study we tested if there were any species-level differences. We used a model similar to that in the second study of this thesis, but added a species-level offset. We show full posterior for the average performance per species and report if contrasts between species are different from zero. The full model definition was:

$$\begin{aligned}
\text{response}_i &\sim \text{binomial}(1,\ p_i) \\
\text{logit}(p_i) &= \alpha_{\text{species}[i]} + \gamma_{\text{behaviour}[i]} + \xi_{\text{individual[i]}} \\
\alpha &\sim \text{normal}(\overline{\alpha},\ \sigma_\alpha) \\
\overline{\alpha} &\sim \text{normal}(-1,\ 2) \\
\gamma &\sim \text{normal}\left(0,\ \sigma_\gamma\right) \\
\xi &\sim \text{normal}\left(0,\ \sigma_\xi\right) \\
\sigma_\alpha &\sim \text{exponential}(1) \\
\sigma_\gamma &\sim \text{exponential}(2) \\
\sigma_\xi &\sim \text{exponential}(2)
\end{aligned}$$

Models were fitted using Stan (Bürkner, 2017) with the *ulam* interface from *rethinking* (McElreath, 2020). We ran 8000 iterations on 4 chains with a warm-up of 500. We monitored Rhat, divergence and effective sample size.

Performance in the delayed repeat test

To test if the different species showed changes in their ability to recall their own behaviour over time, we added one off-set per species on the slope. The rest of the model was similar to that used in the second study of this thesis. The full model definition was:

$$
\begin{aligned}
\mathrm{response}_i &\sim \mathrm{binomial}(1,\ p_i) \\
\mathrm{logit}(p_i) &= \alpha_{\mathrm{species}[i]} + \gamma_{\mathrm{behaviour}[i]} + \xi_{\mathrm{individual[i]}} + \beta_{[i]} * \log(\mathrm{time}) \\
\alpha &\sim \mathrm{normal}(\overline{\alpha},\ \sigma_\alpha) \\
\overline{\alpha} &\sim \mathrm{normal}(-1,\ 2) \\
\gamma &\sim \mathrm{normal}(0,\ \sigma_\gamma) \\
\xi &\sim \mathrm{normal}(0,\ \sigma_\xi) \\
\beta_{[i]} &= \kappa_{\mathrm{species}[i]} + \zeta_{\mathrm{individual}[i]} + \iota_{\mathrm{behaviour}[i]} \\
\kappa &\sim \mathrm{normal}(0,\ \sigma_\kappa) \\
\zeta &\sim \mathrm{normal}(0,\ \sigma_\zeta) \\
\iota &\sim \mathrm{normal}(0,\ \sigma_\iota) \\
\sigma_\alpha, \sigma_\gamma, \sigma_\xi, \sigma_\kappa, \sigma_\zeta, \sigma_\iota &\sim \mathrm{exponential}(2)
\end{aligned}
$$

The model was fitted in a similar way as to the single and double repeat trials models.

“Oblivion is full of memory”

Mario Benedetti

“We do not remember days,

we remember moments.

The richness of life lies in

memories we have forgotten”

Cesare Pavese

Results

Results

Study 1: Long-term memory for own actions in dolphins

Experiment 1: Memory of a single behaviour

All tested dolphins were able to memorize and then recall and perform arbitrarily the previously self-performed actions after very long-time delays (i.e., up to 16 hrs, the maximum duration tested; Performance at 16 hours: mean = 49%, 89% PI = 35-61%; Figure 9A). The performance between the test dolphins and the control dolphins who did not receive extensive training had no statistical differences (Performance at phase 0: : mean = 1.09, 89% PI = -0.14-2.7%; Performance at phase 3: mean = 0.01, 89% PI = -0.64-0.66%; Figure 10). The two control dolphins also recalled successfully in the unexpected single trial after 16-17 hours delay.

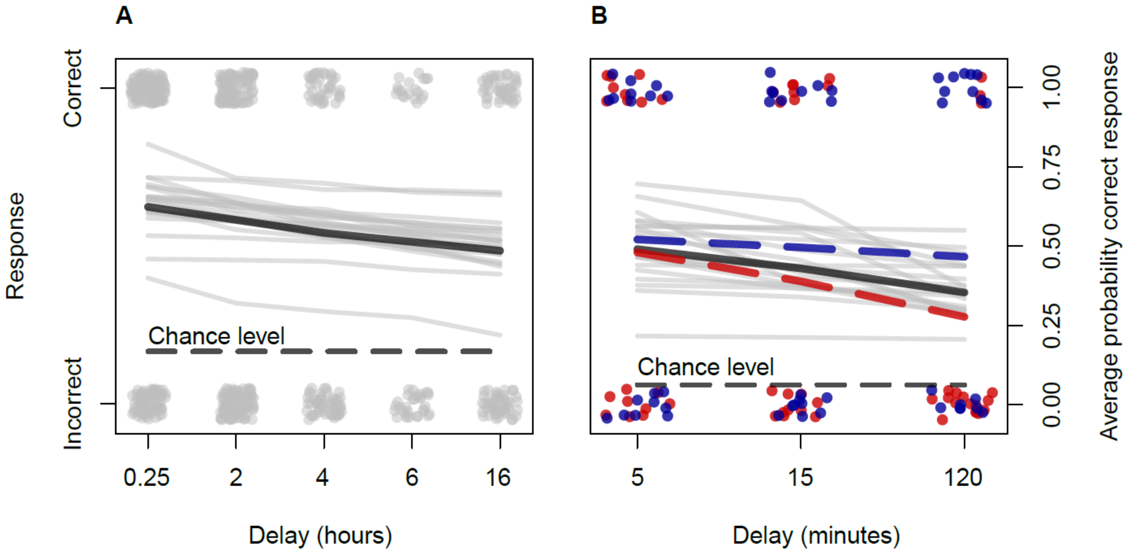


Figure 9. Memory performance for memorized actions. *(A) Memory performance of the test group in trials with a single memorized action. The recall delay for retrieving the memorized action is shown on the x-axis (in hours). The dolphins' response is indicated on the y-axis. Grey dots represent outcomes of trials (correct or incorrect) across all five*

*individuals. The thick grey line denotes model average predictions. Each thin grey line summarizes 20 samples of the posterior. The dashed black line represents chance-level (1/6). (**B**) Memory performance in trials with sequences of two memorized actions. The recall delay for retrieving the memorized action is indicated on the x-axis (in minutes). Average probability of a correct response is given on the y-axis. Blue dots represent outcomes from Karina, red dots from Nemo. Thin grey lines stand for 20 samples of the posterior. Thick grey lines represent model average predictions. Dashed lines represent model average predictions for Karina (blue) and Nemo (red). The dashed black line denotes chance-level (1/16).*

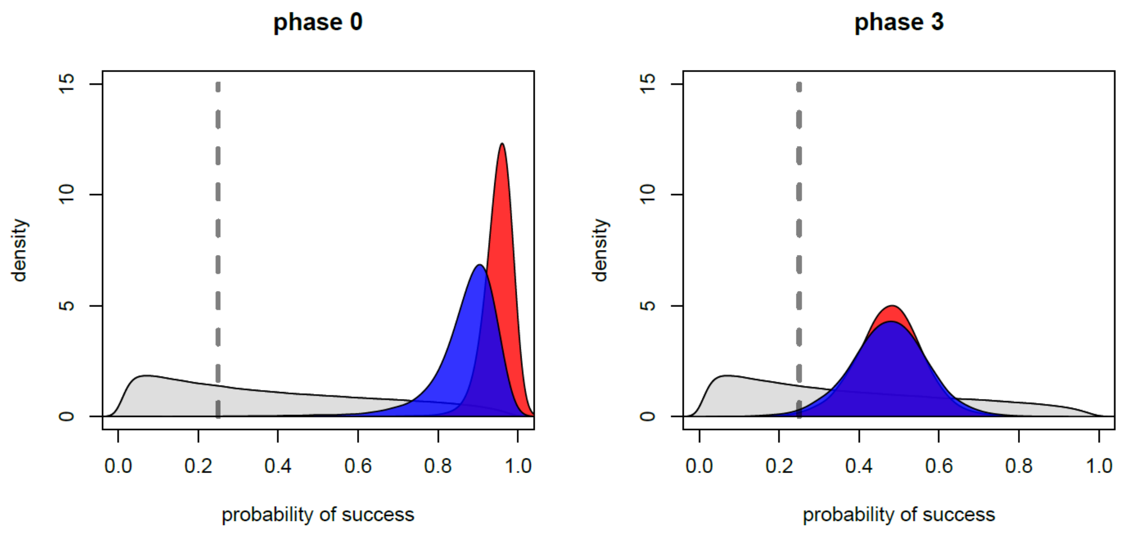


Figure 10. Performance in the single memorize behaviour for test dolphins compare to control dolphins. *Gray density plots show the prior centred around chance-level (grey dashed line). Red coloured density plot shows the posterior distributions for the average performance for the test dolphins and the blue coloured density represents the control dolphins. Phase 0 was the baseline without delays and phase 3 had a delay of 2 hours without distractions.*

Experiment 2 a) Memory of a sequence of two behaviours

The two dolphins tested for sequences of two behaviours were able to remember them for at least one to two hours (Performance at 1-2 hours: mean = 35%, 89% PI = 19-52%; Figure 9B).

Experiment 2b) Memory of a sequence of three behaviours

The two dolphins tested to memorize sequences of three behaviours performed above chance level for at least fifteen minutes (Performance at 15 minutes: mean = 21%, 89% PI = 6-47%; longer delays were not tested due to time constraints). An increase in the complexity of the task in terms of behaviours to be performed in a particular order did not affect their memory performance (β = 0.91 [-0.43, 2.03], Figure 11).

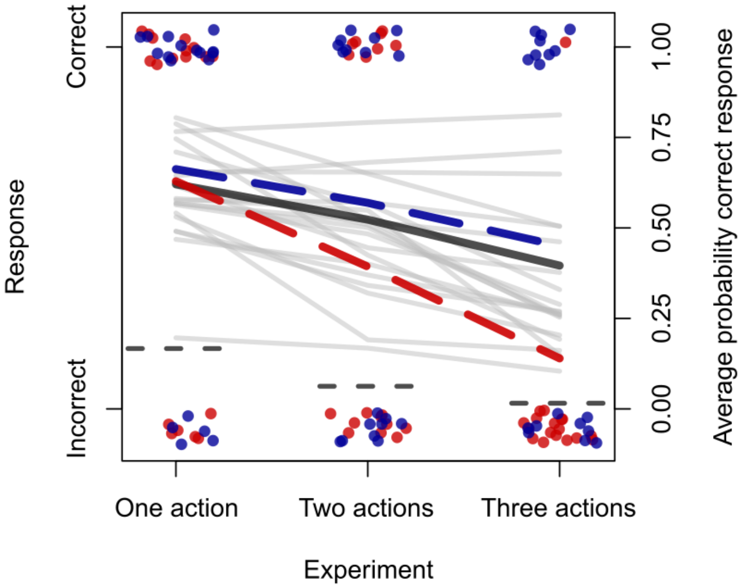


Figure 11. Memory performance for memorized action sequences (increased complexity). *Average probability of a correct response is given on the y-axis. Blue dots represent outcomes from Karina, red dots from Nemo. Thin grey lines stand for 20 samples of the posterior. The thick grey line represents model average predictions. Dashed lines denote model average predictions for Karina (blue) and Nemo (red). The dashed black lines indicate chance-level for each experiment.*

Experiment 3: Reversal of a sequence of two behaviours

Nemo, the dolphin tested to reverse the order of sequences of two behaviours after having self-performed the sequence of two behavioural actions once, was able to reverse sequences of two behaviours above chance level ($\alpha_{reverse}$: mean = 0.48; 5% PI = 0.31, 94% PI = 0.66)

Experiment 3: Memory for commands

The control dolphins were able to perform the action correctly in the short-term memory condition for 6 out of 8 trials. Contrary to this, when a delay of 60 seconds was implemented in the long-term memory condition between the “action command” to memorize and the “go command”, their performance declined to 3 correct trials out of 8 (mean (log-odds) = 1.13; 89% PI (log-odds) = -0.02, 2.54). There was a significant decline in performance for the dolphins when comparing their success after a 60 second delay in trials where the dolphins self-performed the actions, compare to trials with a 60 second delay, where the dolphins needed to remember the hand command and did not perform the action (mean (log-odds) = 2.32; 89% PI (log-odds) = 0.64, 4.13; Figure 12).

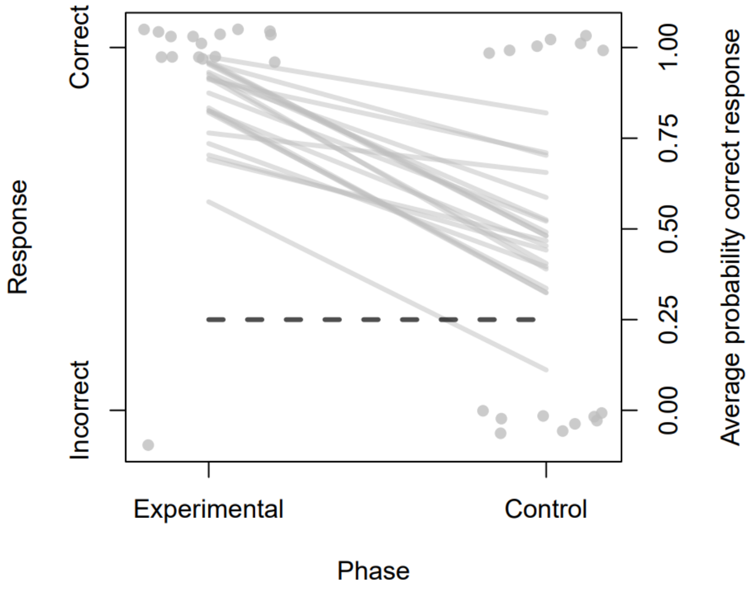


Figure 12. Memory performance for self-performed actions (Experimental) and hand commands of the action to be memorized (Control). *Average probability of a correct response is given on the y-axis. Grey dots represent outcomes from both control dolphins after a delay of 60 seconds when the dolphins performed the action to memorize (experimental) and the dolphins saw the hand command of the action to memorize but they did not self-perform it (control). Thin grey lines stand for 20 samples of the posterior. The dashed black line indicate chance-level.*

The effect of recall latency and distraction during the delay

The test group dolphins' prospective memory performance of recalling a single memorized arbitrary action did not decline significantly with increasing delay (β_{phase}: mean = 0.57; 89% PI = 0.13, 1.02) nor was it affected by distracting activities ($\beta_{distractions}$: mean = 0.16; 89% PI = -0.23, 0.54).

Study 2: Memory for own actions in parrots

Repeat test

Single repeat trials

All parrots showed overall performance well above chance level across all four behaviours, about 75% with a chance level of 25% (see Figure 12) in the single repeat trials. There were no differences between the individuals (sigma: 0.37, 89% PI: 0.02-1.09) and the behaviour to be repeated had little effect on the performance except for ‘Head shake’, which all parrots were less likely to successfully repeat (sigma: 0.80, 89% PI: 0.38-1.44; Figure 14).

Double repeat trials

In the double repeat trials, all three birds also performed well above chance level across all four behaviours with an overall performance of 60% correct and with a chance level of 6.25% (Figure 14). There were no significant differences between individuals (sigma: 0.47, 89% PI: 0.03-1.4) and behaviours (sigma: 0.89, 89% PI: 0.19-1.7).

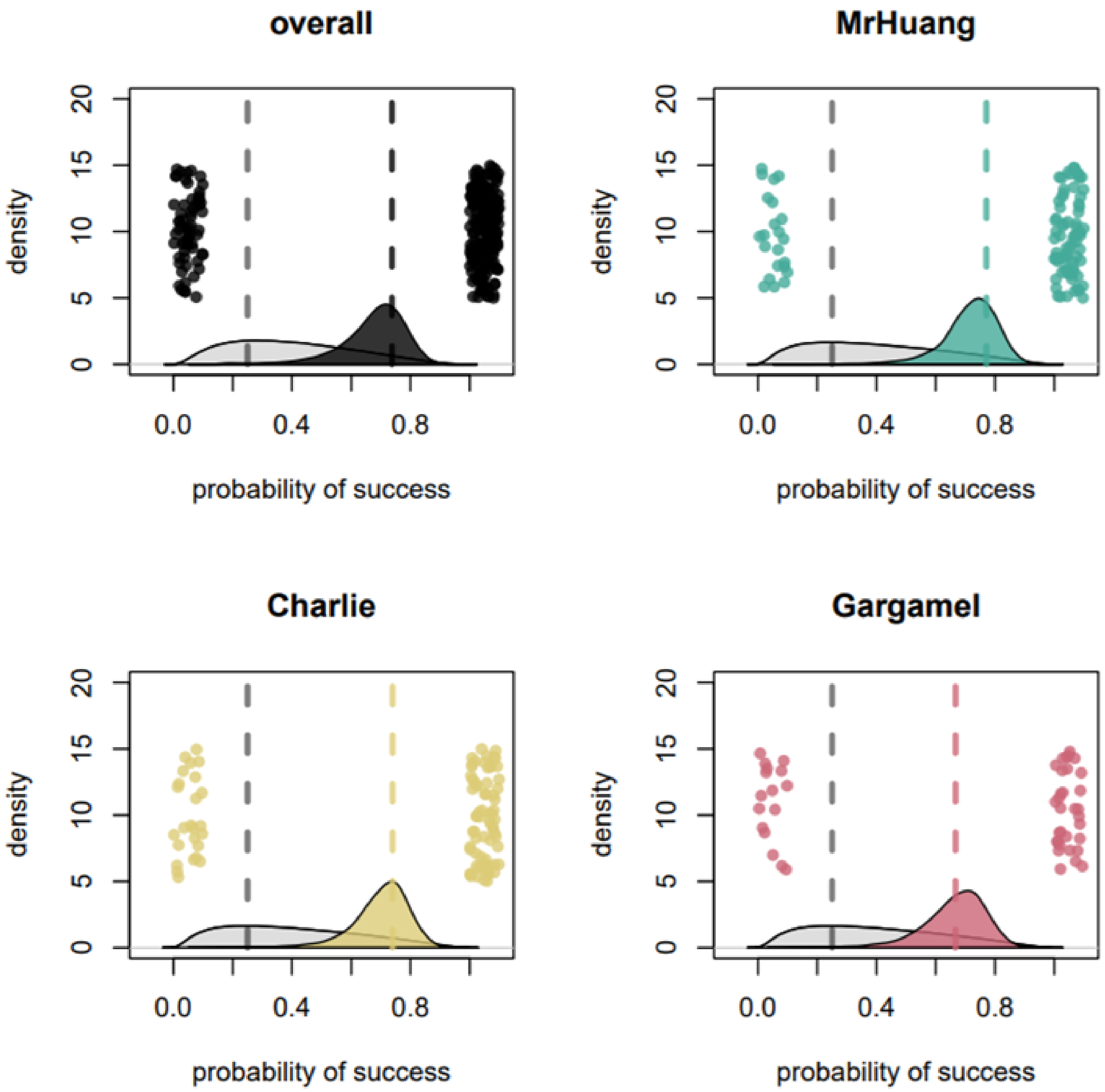


Figure 13. *Performance in the single repeat trials. Gray density plots show the prior centred around chance-level (grey dashed line). Coloured density plots show the posterior distributions for the average performance. Dashed coloured lines are the means. Dots are outcomes per trial.*

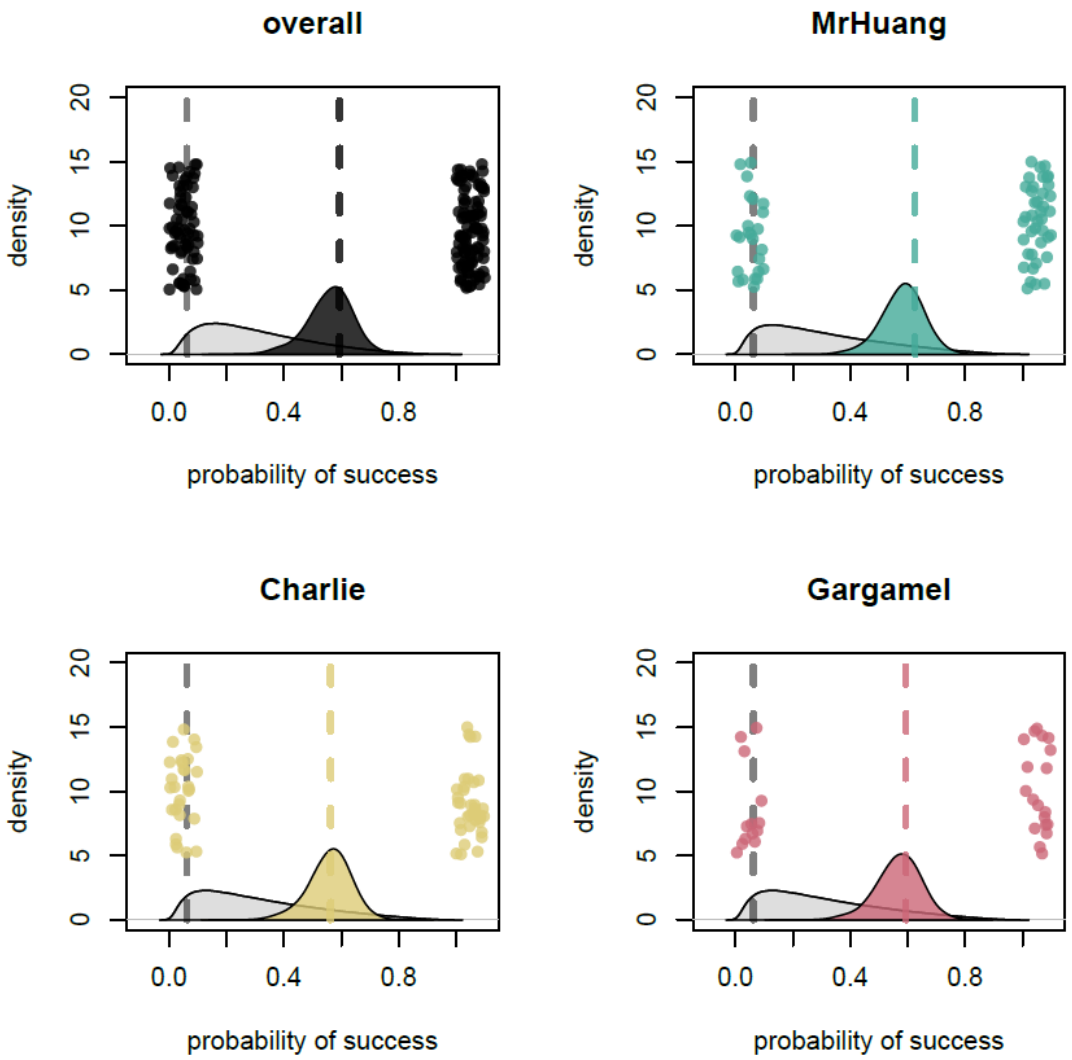


Figure 14. *Performance in the double repeat trials. Gray density plots show the prior centred around chance-level (grey dashed line). Coloured density plots show the posterior distributions for the average performance. Dashed coloured lines are the means. Dots are outcomes per trial.*

Delayed repeat test

Parrots were able to perform above chance level for delays up to 15 seconds (see Figure 15). There were no significant differences between the three individuals (sigma: 0.24, 89% PI: 0.02-0.68) and the four behaviours they had to repeat (sigma: 0.03, 89% PI: 0.03-0.65). The parrots' performance in the delayed (single) repeat test with a corresponding delay of 10 seconds was 41% (0.89 PI: 26-57%).

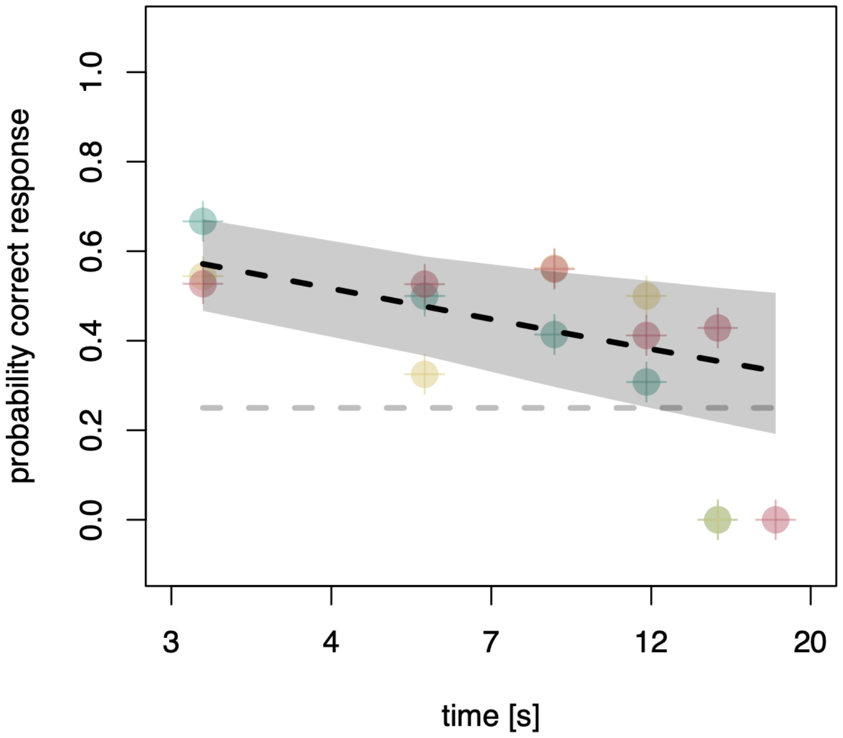


Figure 15. *Performance in the delayed repeat test. Coloured dots are average performance per delay and individual (green – Mr Huang, yellow - Charlie, red - Gargamel). Dashed black line is the predicted performance and grey shaded area the 89% PI. The dashed grey line is the modelled dolphin performance at chance level.*

Novel behaviour repeat test

Table 9 summarizes the animals´ performance in repeating novel behaviours. All three parrots were able to repeat newly learned behaviours spontaneously both in the first test trial and in a second test trial, which was intermixed with already repeated behaviours. "Success" here refers to successfully repeating in both test trials. All three parrots succeeded repeating the behaviour "vocalization". Concerning the second novel behaviour, "lift left leg", only Charlie lifted the correct same leg when asked to repeat, while Mr Huang and Gargamel, lifted the right leg. The last tested novel behaviour, "Move ring into lid", was mastered spontaneously by Mr Huang and Gargamel, who both moved the ring into the lid. Charlie instead lifted the left leg during the session, when asked to repeat the “Move ring into lid”, i.e., he performed the previous learned behaviour. Thus, all individuals repeated two out of three novel behaviours in their first and second trial without training.

Table 9. Summary of the results of the novel behaviour repeat test

Animal ID	**Behaviour**	**Testing date**	**Result**
Charlie	**Vocalization**	**28/06/2021**	**Success**
	Lift left leg	**15/08/2021**	**Success**
	Move ring into lid	16/09/2021	Lifted leg
Mr Huang	**Vocalization**	**30/06/2021**	**Success**
	Lift left leg	15/08/2021	Lifted right leg
	Move ring into lid	**29/09/2021**	**Success**
Gargamel	**Vocalization**	**05/09/2021**	**Success**
	Lift left leg	11/09/2021	Lifted right leg
	Move ring into lid	**04/10/2021**	**Success**

Study 3: Memory for actions in parrots, dolphins, and pinnipeds: a comparative approach

Repeat test

Single repeat trials

Bottlenose dolphins successfully repeated their own actions upon command (average performance: 73%, 89% PI: 59-82%). We did not find statistically significant differences in the performance of single repeat between the five different species (sigma species: 0.33, 89% PI: 0.03-0.83; Figure 15). With all animals' performance being an average of 75% correct. Dolphins and parrots had a chance level of 25% while harbour seals, sea lions and the grey seal had a chance level of 33%.

Double repeat trials

For the double repeat trials, dolphins successfully double repeated with a performance above chance level (average performance: 48%, 89% PI: 34-65%). In this case, there were differences between species (sigma species: 1.02, 89% PI: 0.45-1.75; Figure 16) with dolphins performing worst (45% correct) and harbour seals performing best (91% correct). Dolphins and parrots had a chance level of 6.2% while pinnipeds had a chance level of 11.1%. All five species performed double repeats above chance level.

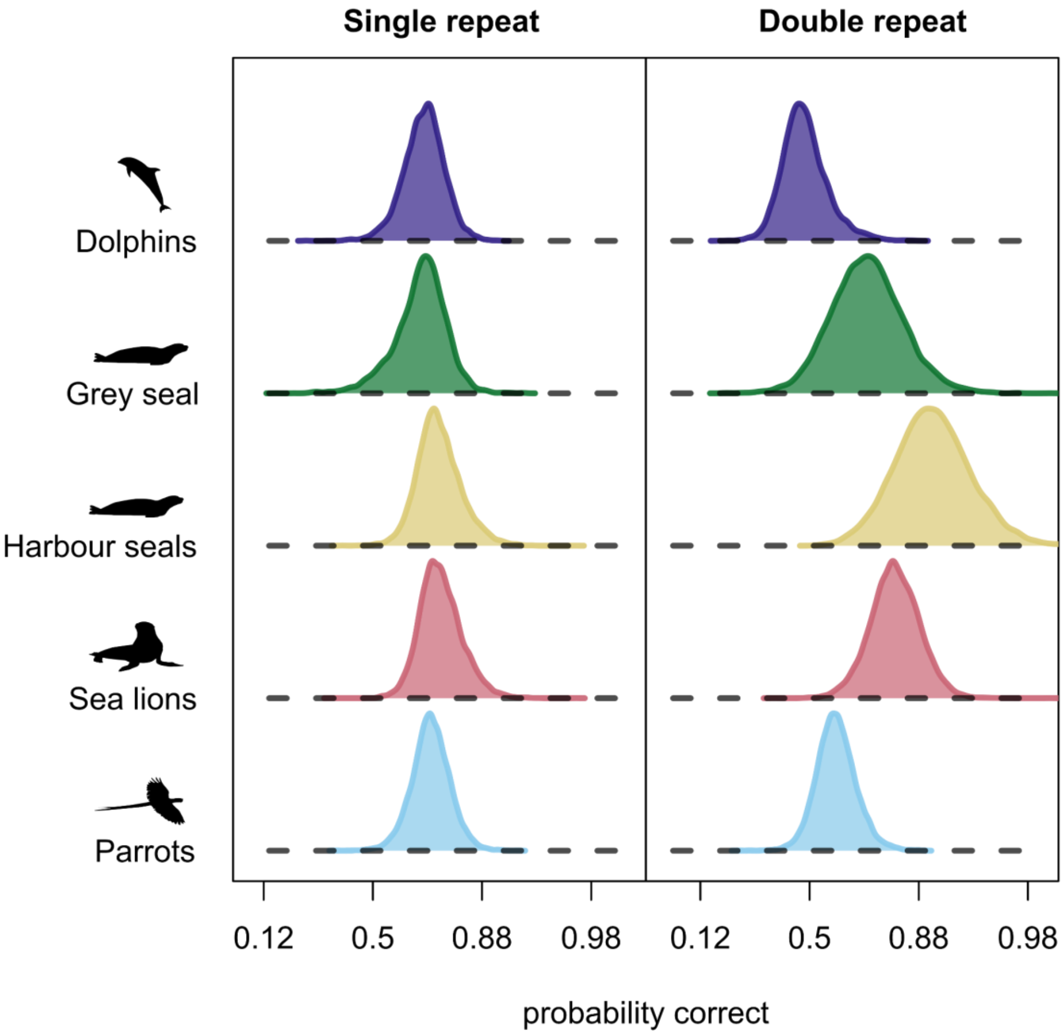


Figure 16. *Performance in single and double repeat trials for the five different species. Dolphins and parrots were tested on four behaviours (25% chance level) and pinnipeds were tested with three behaviours (33% chance level).*

Delayed repeat test

Dolphins reached a maximum delay of 18 seconds. The maximum delay for parrots was 15 seconds, and the pinniped performance varied from 4 to 18 seconds, depending on the individual. All five species were able to perform above chance level for delays up to 12-15 seconds (see Figure 17). There were no significant differences between the species tested (sigma slope species: 0.10, 89% PI: 0.01-0.26; Figure 17).

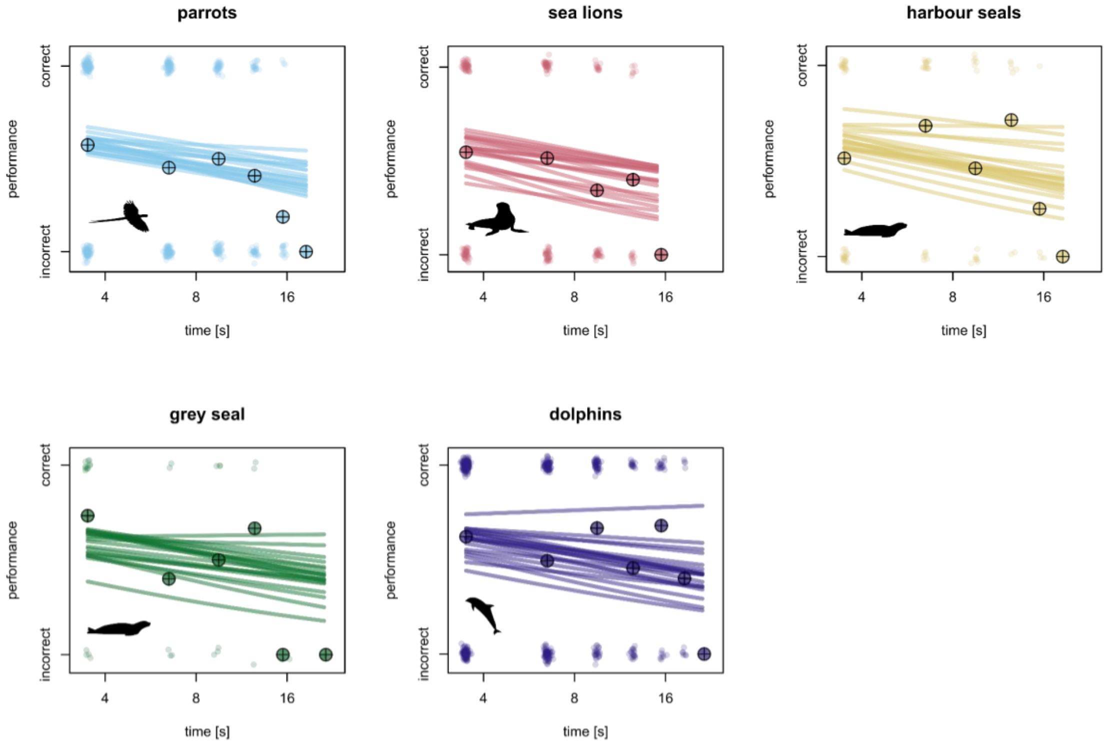


Figure 17. *Performance during the delayed repeat trials. Coloured dots are average performance per delay for all individuals.*

Novel behaviour repeat test

Table 11 summarizes the dolphins' spontaneous performance of repeating novel behaviours at first trial. Two dolphins were able to repeat two novel behaviours without training after having learned to repeat six behaviours with training. In contrast, Achille did not transfer the "repeat rule" spontaneously to novel behaviours. The macaws applied the abstract "repeat rule" straight after the test, i.e., after having been trained to repeat with just four behaviours. Pinnipeds had not been tested for repeating novel behaviours.

Table 11. *Summary of the generalization of the repeating rule experiment.*

Animal ID	**Behaviour**	**Testing date**	**Result**
Clara	Side wave	10/10/2021	Clap
	Tail wave	13/10/2021	Belly up
	Vocal	**17/10/2021**	**Success**
	Chuff	**19/10/2021**	**Success**
Achille	Side wave	12/02/2022	Clap
	Tail wave	15/02/2022	Belly up
	Vocal	**20/02/2022**	**Success**
	Chuff	23/02/2022	Sing
Ulisse	Side wave	09/01/2022	Clap
	Tail wave	15/01/2022	Sing
	Vocal	**22/01/2022**	**Success**
	Chuff	**06/02/2022**	**Success**

“Sometimes you will never know

the value of a moment

until it becomes a memory”

Dr Seuss

Discussion

General discussion

Long-term memory for own actions in dolphins

The results of the present thesis show that dolphins can learn to actively encode and retain previously self-performed actions in their memory for delays of at least 16 hours. Considering the long delays between encoding and retrieval ranging between 15 min and 16 hours and the distracting activities occurring throughout those delays, the memory content must have been processed by the dolphins' long-term memory storage, as the action to be remembered differed from trial to trial pseudo-randomly. For the dolphins to perform above chance level, the subjects had to rely on their memory for the action to be remembered.

The control dolphins also have shown that the information retained in their long-term memory was the self-performed action and not the gestural command given by the trainer. When the dolphins did not self-performed and therefore, experience the event to be remembered, the information of the action to memorized was retained in their short-term memory or working memory, but it was not processed to their long-term memory store.

In a previous study, a single dolphin learned to "repeat" their own previous actions upon command following delays of up to 2 minutes (Mercado et al., 1998). This was taken as evidence that the dolphins encoded their previous self-performed actions episodically. A similar study on dogs however disagreed on the conclusion that the dolphins' encoding could have been accidental because the repeat command was always given in the experimental context and was thus expected, eliciting a "preprogramed response" (Fugazza et al., 2020). These authors did not just repeat the study in dogs, but additionally tested the dogs in everyday situations that were genuinely accidental and still three out of the 10 dogs managed to recall a previous behaviour, non-explicitly encoded, one hour later. This suggests that dogs have a strong capacity for remembering their past self-performed behaviour, which the authors interpreted as evidence for episodic-like memory according to the criteria of answering an unexpected question (Fugazza et al., 2020). The finding that the control dolphins could still remember the encoded action 2 hours and 16-17 hours (overnight) later without ever experiencing a recall test later than 3 min (thus, assumedly, not *expecting* a recall test any later) shows that they encoded the information incidentally, meeting then meeting the criterion proposed by Fugazza and colleagues (2020) for episodic-like memory. The test dolphins had been trained to expect the later recall test of their memorized own actions, and therefore it might be possible that they encoded it in a prospective manner. A comparable example of a human using prospective memory, would be a person driving on a road with the intention of taking a particular exit. Encountering the sign for the respective exit, will trigger remembering to drive out. Similarly, for the dolphins, seeing the "MEMORIZE command" will trigger the retrieval of the appropriate action at that specific moment, but whether the dolphins encoded prospectively (of episodic nature) or purely episodically, cannot be clearly proven with the methodology employed during this experiment. Whether and how the dolphins represent the near or distant "future" in their mind, and what kind of concept the dolphins' ability to memorize actions needed in the future, requires, were not subject of our study and remains difficult to investigate (Clayton et al., 2003; Raby & Clayton, 2009). Yet, our method allowed us to determine arbitrary memory content consisting of specific previously self-performed actions using gestural commands and to cue near or distant future retrieval by a previous experience phase.

Previous episodic-like memory tasks in animals have been criticized for using natural caching behaviour or food availability tasks (Clayton & Dickinson, 1998; Zentall, 2010) arguing that those can be purely instinctive and likely genetically fixed (Gadbois et al., 2015). The task presented in the present study did not depend on timing of food-availability and was not related to natural foraging or any natural behaviours, which could have influenced the dolphins' performance as in previous studies (Naqshbandi & Roberts, 2006; Paxton & Hampton, 2009). Nor were the dolphin's food-deprived for the study during encoding or at retrieval so that their current motivational state could not have impacted their memory function, therefore, the dolphins' performance cannot be explained by automatic preprogramed behavioural responses, also called innate behaviours or instinct (Griffiths & Linquist, 2009; Jaynes, 1956). Innate behaviours are controlled genetically and they do not need to be learned or practice, i.e., mating behaviour of female rats in heat or spiders building their webs (Ross & Denenberg, 1960). Human action planning typically involves a mental ordering of steps required to achieve a goal. Each sequential step later relies on a prospective memory of when those planned actions are to be executed (Altmann & Trafton, 2002). For the first time our study also investigated sequential prospective actions and found the dolphins able to memorize sequences of two actions for at least one to two hours and sequences of three actions for at least 15 minutes. Our final experiment investigated how the dolphins encoded a sequence of actions, namely if they memorize the sequences of two or three prospective and previously self-performed actions a) procedurally, i.e., as behavioural chain represented as a single unit, or b) episodically, i.e., as separated elements in a specific order. For that purpose, we trained the previous two test group dolphins on a new command that required them to carry out the sequence of behaviours they had performed but now in reverse order. One of the dolphins, Nemo, was able to reverse the order of two arbitrary actions after having self-performed the sequence of two behavioural actions once. This suggests that he perceived each action of the sequence as a separate element. He was aware of their order and could therefore reshuffle them in his mind flexibly.

Our results thus show that this individual and perhaps dolphins in general are able to mentally reorder arbitrary sequences of events before acting, an ability previously thought unique to planning by mature humans (Einstein & McDaniel, 2007; Kvavilashvili et al., 2001; Raby & Clayton, 2009). At the same time, it provides more evidence that the dolphin are remembering the events episodically. Episodic memory is said to require the ability to subjectively sense time. This ‘subjective sense of time’ provides the knowledge of one's personal past, defined as episodic memory, and the ability to keep track of the order of events experienced by the individual, and the knowledge of what comes before and after (McCormack & Hanley, 2011). The ‘subjective sense of time’ will allow the individual to also ‘think about’ and ‘plan for’ the future, which is defined as ‘prospective cognition’. Considering the arguments above, episodic-like memory could then be used to remember the order of experienced events, the ‘temporal order memory’ which would make it possible to prepare for a future need or to solve a current problem. Nemo could reverse the order of two behaviours, showing that he represented the order of the events and showed potential understanding for what comes before and after (McCormack & Hanley, 2011). In addition to being crucial for episodic-like memory, it is a core component of planning, which requires stepwise ordering of prospective actions to achieve a future goal (Altmann & Trafton, 2002; McColgan & McCormack, 2008). Adult humans both order and reorder events mentally before acting (Einstein & McDaniel, 2007; Kvavilashvili et al., 2001; McColgan & McCormack, 2008), abilities that children under the age of five generally lack (McCormack & Hanley, 2011). This suggests that the memory content is not procedural but episodic in nature as it contains particularities of an event (i.e., previous self-performed actions) ordered in time.

A possible evolutionary explanation for the dolphins’ episodic-like memory and potential prospective memory abilities may relate to their complex socio-ecological environment and behaviour. Dolphins live in fission-fusion societies considered complex (Lusseau, 2003) and display collaborative hunting (Jaakkola et al., 2021, 2021), the most complex form of hunting where different individuals acquire and maintain different roles throughout the hunt (King, Connor, et al., 2021; Torres Ortiz et al., 2021). Also, dolphins communicate to synchronize their actions in cooperative tasks (King, Guarino, et al., 2021), so they might need to represent and plan the steps depending on those of different individuals for their hunts, reorder them when necessary and possibly share that information.

Another possible adaptive value of the dolphins' memory capacity, in particular their flexible memory for (prospective) action sequences, relates to their complex communication system (Herman, 1980). Dolphins are vocal learners and able to imitate and innovate acoustically (Herman, 2002; Richards et al., 1984). They exhibit cultural variation of vocal repertoires (Henderson et al., 2011; Whitehead et al., 2004) and produce individual whistles by which they recognize and address other individuals (King & Janik, 2013). Dolphins' whistles consist of multiple components and it is possible that adding on or reversing whistle components changes the meaning. Representing, ordering and reordering sequences of events might form part of their communication system. Yet, even though, dolphin communication is assumed to be complex, based on their enormously variable, culturally distinct (Henderson et al., 2011; Herman, 1980) and to date undecipherable vocal repertoire, little is known about its structure, meaning and use (Janik, 2013).

Dolphins, as modern cetaceans, have evolved separately from primates for at least 92 My (Kumar & Hedges, 1998). Like primates, they have a brain markedly larger than expected for their body size (Marino, 2002; Marino et al., 2007). It has been suggested that they have evolved a level of complex cognition comparable to that of great apes, corvids and parrots (see Osvath et al., (2014) for review). The results of our study support this further. Prospective memory and cognition had not previously been studied in dolphins, but they turn out to be an interesting model for studying the evolution prospective cognition and mental time travel.

Our novel method for investigating encoding of episodic-prospective self-performed actions can be directly applied to a broad range of vertebrate taxa, particularly those already considered to exhibit complex cognition, namely corvids, parrots and primates, and can thus be used for systematic cognitive comparisons. It therefore opens new avenues for unravelling the evolution and mechanisms of prospective cognition and its role in the evolution of general intelligence.

Short term memory for own actions in parrots and dolphins

The blue-throated macaws and dolphins tested in this thesis could recall their own previous actions well above chance levels. The data on parrots provided the first evidence for mental representation and memorization of their own actions in an avian taxon. The overall (single) repeat performance of parrots was similar to those of mammals, and the dolphins tested. Fugazza and colleagues (2020), hypothesized that one of the building blocks of the supposedly complex ability to represent the self might be the capacity to mentally represent one's own behaviour. Our study shows that this ability is also present in parrots and dolphins and therefore is not only restricted to mammals but has also evolved in birds too.

This is an interesting finding considering the evolutionary distance between mammals and birds. Birds also have differently structured brains compared to mammals although their forebrain (nido- and mesopallium) represents a homologous structure to the mammalian neocortex (N. J. Emery & Clayton, 2005b; Gutiérrez-Ibáñez et al., 2018;

Jarvis et al., 2005; Smeele et al., 2022). Like the neocortex, this telencephalic structure fulfills higher cognitive functions even if it lacks the cortex-typical lamination and is structured differently (Kirsch et al., 2008). Even though parrots' brains may be small in absolute size, their relative brain sizes stand out amongst all vertebrates like otherwise only those of corvids, primates and dolphins (Osvath et al., 2014). Additionally, parrots exhibit an astonishing neuronal density in their pallium with neuron numbers exceeding those of primate species (Olkowicz et al., 2016). It may be the large absolute numbers of telencephalic neurons in their pallium that explains their advanced behavioral and cognitive complexity (Dunbar & Shultz, 2007; N. J. Emery & Clayton, 2005a; Olkowicz et al., 2016). Together the architectural differences in the brains of mammals and birds, and the great evolutionary distance indicate that the ability to remember their own actions is likely a result of convergent evolution.

The finding that the birds performed above chance level and similarly well in single and double repeat trials suggests that the birds relied on their memory of their last own previous action, rather than the last command (i.e., the previous hand signal) they received. The interval between the command for a behavioral action and the second repeat command was on average 10 seconds. If the parrots were remembering the hand gesture, their performance of the second repeat should have been similar to the performance of the delayed condition at 10 seconds (Figure 2AB). However, the parrots' performance in the delayed (single) repeat test with a corresponding delay of 10 seconds was 20% lower compared to their performance in the double repeat. It is therefore unlikely that the parrots remembered the last command rather than responding to the repeat command. The better performance at double repeating compared to remembering following a delay of 10 seconds, suggests that the parrots remembered their last action, which was performed only 5 seconds earlier, rather than the last command.

For the dolphins, their performance during the double repeat trials was unexpectedly lower than during single repeats. This finding could be interpreted as if the dolphins were indeed trying to remember the most recently presented gestural command, rather than their most recent own behaviour.

Our other objective was to examine whether the parrots had actually abstracted the underlying rule of repeating their last performed action, which can be considered as an abstract concept (Scagel & Mercado III, 2022). The parrots had been trained with four behaviors only before it was tested whether they had learned the “repeat” rule and could transfer it to novel actions they had not repeated before (novel behavior repeat test). Their spontaneous success shows that indeed they had generalized the repeat rule. For dolphins, they needed to be trained for six behaviours instead of four in order to generalize the rule, and in fact, one of the dolphins, Achille, was not able to perform this generalization. The fact that parrots and dolphins learned this abstract concept after only being trained for four actions is remarkable. By comparison, pigeons, monkeys, parrots and corvids require thousands of trials to learn the same-different concept required to succeed in match-to-sample tests (Smirnova et al., 2021; Wright & Katz, 2006), or sea lions need over two thousand trials to form equivalence relations, where the animal needs to spontaneously transferred the relationship on a set that is reflexive (A ~ A), symmetric (if A ~ B, then B ~ A) and transitive (if A ~ B and B ~ C, then A ~ C; Kastak & Schusterman, 1994; Schusterman & Kastak, 1993). In general, conceptual ability provides great efficiency to learning (Zentall et al., 2008). Fast concept learning and generalization may be adaptive under many circumstances as it allows the individual to apply prior learning to a new environment avoiding the costs and risks associated with new trial-and-error learning (Zentall et al., 2008). Why parrots showed such rapid concept learning ability, needs to be solidified by further direct comparisons of different taxa in the same tasks and remains speculation until it is investigated further. Maybe parrots need to adapt fast to novel environments or social constellations but the same is likely true for primates and pinnipeds (Marino, 2002; Smeele et al., 2019) and further study is required.

The other important conclusion one can draw from the parrots' spontaneous transfer ability is that they could recall their own previous behavior without being trained to do so. Given that the repeat command was never associated with novel actions, we can assume that they did not expect the repeat command after the novel action in the experimental test. According to Fugazza and colleagues (2020), the unexpectedness of the test rules out a "prepared behavioral response" explanation and suggests accidental encoding of the memory (Fugazza et al., 2020). In our experiment, it can be assumed that repeating the novel behavior is unexpected by the parrots and dolphins. Firstly, because the novel behaviors were never asked to be repeated, and secondly, only in the case of the parrots, because of the long break between the delayed repeat experiment and the novel behavior repeat test (~45 days). Accordingly, the parrot's success in retrieving the memory of the novel behavior would have to be explained by episodic-like memory. Of the four previously tested mammalian taxa, only dogs have been tested for accidental encoding (albeit with substantially longer time scales; Fugazza et al., 2020) and only dolphins and dogs were shown to generalize the repeat command to new behaviors (Fugazza et al., 2020; Mercado et al., 1998; Scagel & Mercado III, 2022). The pinniped species were not tested in this respect and the macaques were not able to transfer the repeat rule having been trained with three behaviors only (Paukner et al., 2007; Smeele et al., 2019). The dolphins (Mercado et al., 1998; Mercado III et al., 1999) transferred the repeat rule to new behaviors but already knew the repeat command for a long time and there is no information on how many behaviors they required to learn the repeat rule before they were capable of generalizing. Both dog studies (Fugazza et al., 2020; Scagel

& Mercado III, 2022) reported that the subjects were able to transfer the repeat rule after they had trained the repeat command on six to seven behaviors. Although the data on the different species are not directly comparable due to the differences in methodology, particularly concerning the previous training exposure, our results suggest that parrots have a capacity to generalize abstract rules comparable to big-brained mammals as dolphins in the same paradigm. Domestic dogs which also generalized well, may represent a special case because of domestication and enculturation (Huber et al., 2014; Schmidjell et al., 2012). For instance, studies on wolves raised by humans and dogs with little human contact showed that dogs were still better at reading human communicative gestures, suggesting that artificial selection for a set of social-cognitive abilities enhanced their responsiveness to human communicative signals (Hare et al., 2002). Similar findings have been reported in birds as well, e.g., artificial selection negatively affecting spatial learning ability in white leghorn chicken compared to their ancestor the red jungle fowl (Lindqvist & Jensen, 2009). In any case, such effects of artificial selection and enculturation should be considered in phylogenetic comparisons of cognitive abilities and may explain why dogs performed well in this task.

Concerning the duration of memory retention, our results show that both, parrots and dolphins could remember their own behavior for up to 12-15 seconds. The retention interval is similar to those previously reported in the wide variety of species tested in Delayed-Match-to-Sample, a common paradigm to test animals’ working memory (Lind et al., 2015; Pack et al., 1991). Our results are also quite similar to those reported in pinnipeds and macaques tested previously in this paradigm (Mercado III et al., 1999; Paukner et al., 2007; Smeele et al., 2019) but dogs exhibited longer retention intervals. These differences can be explained by methodological differences. In one of the dog studies, the delay intervals were fixed with 10 and 30 seconds, in our case, if the subjects made a mistake, the interval will decrease 3 seconds so that the parrots were never exposed to such long intervals (Scagel & Mercado III, 2022). In the second dog study, the trial for the delay condition only contained a single action that had to be repeated after 1 hour (Fugazza et al., 2020). For our study, each experimental session had 16 trials, which adds noise into their memory system increasing the attention needed to performed correctly (Fugazza et al., 2020). As parrots paralleled other mammal species, including the tested dolphins in this experiment, in performance for single and double repeats, it is likely that the reported differences are a result of different methodology. Unfortunately, details of the training methodology of the previous studies are unknown. Replicating the previous pinniped study in this respect, the parrots and dolphins were not trained for expecting the delays before entering the delayed repeat test, so it was tested how well they remembered when not actively trying to remember. Concerning the dogs, in contrast, no details are given as to whether the delay was learned with training steps gradually increasing in duration, or whether the animals were directly tested at their longest retention durations in an unexpected manner. The same challenge is present when comparing results of Delayed-Match-to-Sample tasks, as the amount of training is not always reported accurately, or at all, making species comparisons in memory performance very challenging (Lind et al., 2015).

The incredibly complex brains of humans and varied faculties are likely to have evolved from simpler prototypes of our ancestors (Bennett, 2021). Paul Cisek developed the theory of “phylogenetic refinement” where behaviors and brain structures are the consequence of evolutionary refinement from more basic building blocks (Cisek, 2019). One may see the parrots’ ability to represent and remember their own actions as an important building block of the ability to represent ‘the self’ (Fugazza et al., 2020). In order to experience one's self in the past one would need an awareness of self also in the present time (Zimmer et al., 2001). Thus, the parrots could be considered have evolved a prerequisite of episodic-like memory. Fugazza and colleagues (Fugazza et al., 2016, 2020) state that previous studies can be explained by a “prepared behavioral response” by the subjects as they expected the repeat command to be given. We argue that the repetition of a novel action can be considered as accidental encoding in our study given that the experimental animals had never been asked to repeat those actions before. Additionally, the test of the first untrained action for the novel repeat test took place following a ~45-day break for the parrots after the delayed repeat test had been completed, so that the they were not in a repeat testing routine anymore.

Like most parrots, blue-throated macaws are very social, show fission-fusion dynamics with temporally changing flock composition (e.g., for foraging or during certain developmental phases (Herzog et al., 2021)) and live in long-term monogamous pairs throughout their lives (Toft & Wright, 2015), all of which likely has selected for socio-cognitive adaptations and even larger relative brain sizes (Dunbar & Shultz, 2007; N. J. Emery, 2006). Being able to remember one’s own behavior may be equally adaptive for species living in complex societies (Merkle et al., 2015; Osvath et al., 2014) than remembering the behavior and interactions of third-parties (Dunbar & Shultz, 2007; Kamil & Roitblat, 1985; Stevens & Gilby, 2004). Concerning parrots, remembering one’s own past action might be particularly important for coordinating cooperative behaviors with one’s mate (e.g., when jointly rearing offspring (N. J. Emery & Clayton, 2005a)) or group members (e.g., when foraging individuals of a flock leave to join other groups (Bradbury & Balsby, 2016)), for which parrots exhibit the cognitive and motivational basis (Brucks & von Bayern, 2020; Krasheninnikova, Brucks, Blanc, et al., 2019; Krasheninnikova, Brucks, Buffenoir, et al., 2019; Ortiz et al., 2020; Tassin de Montaigu et al., 2020). Parrots also have been shown to display capacity for reciprocity, which may require long-term episodic memories of own and others' behavior (Brucks & von Bayern, 2020; Krasheninnikova, Brucks, Blanc, et al., 2019; Stevens & Gilby, 2004) for the reciprocal sharing of resources.

Dolphins are also highly social and live in complex fission-fusion groups. Dolphins can greatly benefit from remembering their own actions in terms of social behaviour and foraging behaviour. Dolphins off the coast of Australia will carry sponges to protect their rostrums from sea urchins, a behaviour that has been shown to be culturally transmitted (Smolker et al., 1997). Remembering the advantages of this type of actions would explain the diversity of their culturally transmitted behaviour (Whitehead et al., 2004). Another example is the "mud-ring behaviour" observed in Caribbean waters, where dolphins will search for prey in shallow waters and create a mud-ring by slapping the sea bottom with their flukes (Ramos et al., 2021). This will create an anoxic environment for the fish, making them jump out the water, where the dolphins are waiting with open mouths.

In summary, blue-throated macaws and dolphins were proficient in learning and generalizing the abstract concept of "repeat my most recent action". Our results show that parrots and dolphins are capable of reporting their own previous actions upon command. They therefore exhibit a pre-requisite for self-representation and for episodic-like memory, previously only shown in social, large-brained, domesticated or enculturated mammals. Given the evolutionary distance between mammals and birds (Osvath et al., 2014) with a common ancestor around 296 mya (Osvath et al., 2014), this ability is likely to constitute an example of convergent or independent evolution, due to similar selection pressures (Baciadonna et al., 2021; Clayton et al., 2001; N. J. Emery & Clayton, 2005a; Osvath et al., 2014). Our study provides new insights into the independent evolution of functionally equivalent building blocks of self-representation and episodic-like memory in distantly related taxa (Conway, 2005; Suddendorf & Corballis, 2007).

Comparative memory between distantly related species

In the studies conducted in this thesis, we trained and collected the short-term memory for actions data with comparable methods in all animal species. In our results, dolphins showed a very similar performance level to a parrot species and three species of pinnipeds, confirming that basic self-representation and episodic-like may be adaptive for species living in complex societies. All five species learned to repeat their own behavior upon command. Their performance was equal in single repeat trials as well as in delayed trials, in which all 5 species mastered a maximum delay of 12-15 sec. This finding is also in line with the previous studies that employed different procedures. Macaques are also social (and fairly large brained) and also dogs. Dogs often perform better than one would predict from their smaller relative brain size which might be explained by effects of enculturation and domestication. Differences in delay trials had been previously reported by Mercado et al. (1998) with dolphins mastering retention intervals up to two minutes. Yet, it remained unknown how the dolphins had been trained and how much exposure they have had to the command and the delay before the experiment. It is possible that much more effort was put into training the dolphins gradually to respond to greater delays, whereas the species tested in this study was tested on the delay repeat condition without previous experience. In our study, dolphins had been trained a similar number of training sessions as the parrots and pinnipeds. The dolphins used in this study were also not familiar with the repeat command, and they learned following the same training steps as the parrots and pinnipeds.

We only found differences in the double repeat trial, with parrots and pinnipeds performing significantly better than dolphins. These results can be due to the parrots and pinnipeds remembering their own actions, while the dolphins were trying to the remember the gestural command of the trainer instead. Our results highlight the importance of consistent methodology for comparing the performance of different species in cognitive tasks directly in order to draw conclusions about interspecific differences.

Comparative cognition allows us to gain insights in the cognitive evolution of a trait enabling us to better understand how these abilities evolved (Lambert et al., 2022). This is achieved by comparing similarities and differences across a wide range of closely and distantly related species (Aguenounon et al., 2020; Krasheninnikova et al., 2020; MacLean et al., 2014). To compare performance in different species is crucial to follow experimental methods as closely as possible for direct replication (Farrar et al., 2020). One of the weaknesses in comparative cognition is the lack of comparability of the results caused by an insufficient level of standardization of the methodologies (Krasheninnikova et al., 2020).

When distantly related animals share similar socio-ecological problems, analogous adaptations may evolve independently resulting in similar solutions (Keeton & Gould, 1986). The last common ancestor shared between birds and mammals, a stem amniote, lived around 296 mya (Osvath et al., 2014). A case of convergent evolution becomes stronger the more phylogenetically separated the groups are (Papini, 2002), as it is in our study. The results of our study support three different possible evolutionary pathways. Either the building blocks of episodic-like-memory and self-representation (1) evolved early in vertebrate evolution being shared at least between mammals and birds, or (2) it is a shared trait within mammals and convergently evolved in (some) avian groups, or (3) it evolved multiple times convergently within mammals and birds exhibiting a high degree of social complexity.

Parrots, dolphins and pinnipeds have adapted to very different environmental requirements through a long independent evolutionary path (Bradbury & Balsby, 2016; Osvath et al., 2014; Smeele et al., 2019). In the case of dolphins and parrots, even though their brains are structurally very different, both species share similar life histories (Kirsch et al., 2008; Marino et al., 2007; Osvath et al., 2014). Dolphins and parrots have complex social groups with fission-fusion dynamics, were individuals shift groups, groups can merge or divide, and for both species, being able to keep track of their social interactions would be beneficial in terms of fitness (Bradbury & Balsby, 2016; Connor et al., 2000; Merkle et al., 2015). Both species have shown collaborative abilities and the understanding of their partner role in cooperation tasks (Jaakkola et al., 2018; Ortiz et al., 2020). Both species also have complex communication systems and share the unique trait of being open vocal learners, and great imitators (Balsby et al., 2012; Balsby & Adams, 2011; Bradbury & Balsby, 2016; Herman, 2002; Richards et al., 1984). Dolphins and parrots have shown to have signature signals that can be used for individual identification, where memory will also play a fundamental role in this case (Balsby et al., 2012; King & Janik, 2013). Dolphins and parrots have a long developmental period after birth, before they are totally independent with macaws depending on their parents with periods up to 11 to 14 months (Forshaw, 1991; Parr & Juniper, 2010), and dolphins nursing for periods up to 3 years and both species also have great longevity (Mann, 2009; Smeele et al., 2022). With a potential long lifespan, animals have the opportunity to learn, explore and understand their environment and use their great cognitive abilities throughout their long lives. Parrots and dolphins have also the ability to use and create tools, a very rare trait among animals which is related with goal-oriented behavior and future planning (Auersperg et al., 2014; Krützen et al., 2005; Smolker et al., 1997). For pinnipeds, there are major differences. Sea lions have harems between five and 15 females, and parental care has a longer duration compared to seals, with their pups lactating for periods up to a year (Cappozzo & Perrin, 2009; Cornet & Jouventin, 1980). For seals, the strategy is completely different: seals would fast for a few weeks and stay with their pups feeding them continuously. After seal pups have enough fat, they are left alone to forage for themselves (Cornet & Jouventin, 1980). Sea lions are considered more social than seals and group hunting has been reported for some species (Burns, 2009; Sepúlveda et al., 2007; Wursig & Perrin, 2009). Pinnipeds and dolphins have in common that they are both mammals and therefore, their brain architecture is more similar, compare to parrots. These differences in ecology between pinnipeds, parrots and dolphins made us expect dolphins and parrots to perform best, followed by sea lions and lastly seals both for reporting their own actions and in memory for their own actions. Despite the differences, all species tested are social and therefore, our results support the hypothesis that social complexity may select for self-representation and episodic-like memory. Studies on non-social mammals and birds are necessary to compare performance in social vs. non-social animals and support our findings.

In conclusion, our study supports that sociality may be an evolutionary driver. It also shows that the previously reported differences in memory performance between the different animal species can be explained in terms of training and previous experiences. The five species in our study showed similar performance when trained and tested under comparable conditions, independently of their brain size, social organization, ecological pressures of evolutionary distance. Training animals to repeat their own actions is a very promising method to study episodic-like memory and the building blocks for self-representation, but more species need to be tested in order to draw conclusions about the evolution of the building blocks of episodic memory and the representation of the self.

Conclusion

With this thesis I have contributed to the field of animal memory and comparative cognition by providing first data on parrots and applying new methodologies. In the first chapter, we actively asked dolphins to remember specific behaviours from their repertoire, to my knowledge this methodology has never been applied to another animal species, finding out that dolphins do have long-term memory for self-performed actions. With the first study, we could also show that dolphins can remember sequences of actions, and that the elements of the sequences are encoded as individual elements, which order, can be reversed by at least, the tested dolphin, and potentially within the capacity of the species. In the second chapter, I used a previously tested memory paradigm in a novel taxon, the parrots, testing for the first time an avian species, distantly related to the previously tested mammals. In this chapter we tested an avian species for the first time in a memory task and could conclude that parrots, similarly to previously tested mammals, show remarkably comparable memory abilities for self-performed actions. Finally, in the last chapter, I used the same methodology applied to the parrots on dolphins, to test in a directly comparative manner for the first time both species trying to draw conclusions on the evolutionary selective pressures of episodic-like memory and the building blocks of self-representation. The surprisingly similar performance in all different taxa reveals that the previously reported differences in memory for own actions are most probably due to differences in methodology and training procedures. All tested species showed similar performance in memory. Despite of being relatively distantly related (and concerning the mammal-bird comparison extremely distantly related) they were all social raising the possibility that social life selects for the building blocks of self-representation and episodic-like memory.

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