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Bobrowicz, Katarzyna

2019

Document Version:
Publisher's PDF, also known as Version of record

Link to publication

Citation for published version (APA):
Bobrowicz, K. (2019). *Memory for Problem Solving: Comparative Studies in Attention, Working and Long-term Memory*. [Doctoral Thesis (compilation), Cognitive Science]. Department of Philosophy, Lund University.

Total number of authors:
1

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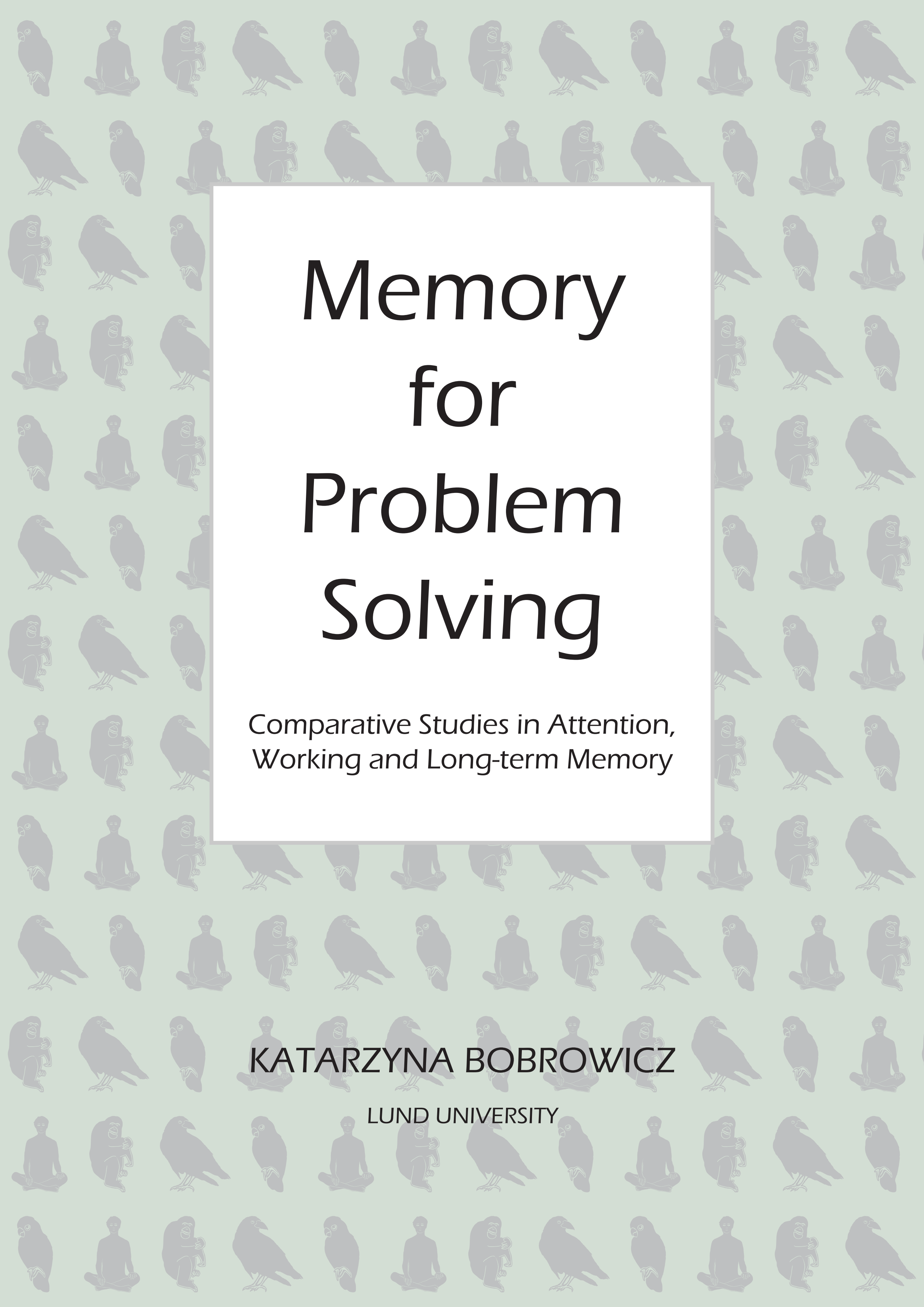

Memory for Problem Solving

Comparative Studies in Attention, Working and Long-term Memory

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Cognitive Science

Lund University Cognitive Studies 174
ISBN 978-91-88899-57-6
ISSN 1101-8453

Printed by Media-Tryck, Lund 2019 NORDIC SWAN ECOLABEL 3041 0903

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Cover by Ryszard Bobrowicz

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ISBN 978-91-88899-57-6 (print)
ISBN 978-91-88899-58-3 (pdf)
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Printed in Sweden by Media-Tryck, Lund University
Lund 2019

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MADE IN SWEDEN

Acknowledgments

During the last four years, I have met many people and animals, without whom I would have much less to present in this thesis. I will be forever grateful to everyone who was kind to me on the way, and I hope that no one will be left unacknowledged by the end of this list.

First and foremost, I would like to thank Ryszard Bobrowicz for his continuous support, from finding this PhD position and leaving our previous lives behind, through bearing with my frustrations, to reading everything that I wrote during these years and providing me with a multitude of priceless feedback.

Second, I would like to acknowledge my supervisors: Mathias Osvath, Mikael Johansson and Elia Psouni. I thank Mathias for giving me the opportunity to pursue doctoral studies. I am thankful for my discussions with Mikael, and his tremendous help at those points of my studies, at which nothing seemed to be going well. Huge parts of this thesis would not be here, if it was not for those challenging discussions. I am also thankful for my cooperation with Elia who helped me stand on my own feet, supported me research-wise, and showed me how to lead a group in a decisive yet respectful way.

Furthermore, I am grateful to Helena Osvath, Tomas Persson, Gabriela-Alina Sauciuc and Megan Lambert. I could never work with ravens, if it was not for Helena's efforts and time, and likewise, I could never work with chimpanzees and orangutans, if it was not for Tomas and Gabriela who watched out for me in the Furuvik zoo. Without Megan, two years of my studies would not be the same, as she brought great warmth, passion for working with animals, and valuable feedback on my experimental setups and manuscripts.

I would like to thank my co-authors: Alice Auersperg, Mark O'Hara and Chelsea Carminito. I owe my work with Goffin's cockatoos to Alice, who introduced me to the flock, provided continuous support and trusted me with the well-being of her animals. I am thankful for Mark's great and rapid help despite the huge distance that divided us most of the time, and I am thankful for Chelsea's spirit, passion and skill that she put into our project.

All these studies required a huge support of Tomas Persson, Anna Cagnan Enhörning, Tobias Hansson Wahlberg, and Anna Östberg, who all helped me navigate through the world of administrative issues throughout my studies. I am

grateful to all of them for bearing with my never-ending questions, and doing it so kindly. Without them, many of the opportunities would have slipped through my fingers.

Although my work with animals would not be possible without all of these colleagues, I would like to acknowledge all people that are not academics, but are nevertheless passionate about animals, and express it through working in the zoological gardens: the Furuvik zoo, Skånes Djurpark, and Zoo Nowy Tomysl. Special thanks must go to: Daniel Hansson, Linda-Marie Lenell, Elina Lundholm, Natalie Magnusson and Lotta Widlund, who all contributed to my work in the Furuvik zoo; to Erik Nilsson, Malte Nilsson and Magnus Wildt, who helped me at Skånes Djurpark; and to the staff at Zoo Nowy Tomysl, especially Pani Mirka and Pani Ania, whose surnames I missed just like I miss the great fun that we had, when working together in the park.

I am thankful to all people who allowed me, in one way or another, to meet all the animals that I have met since I started my studies in 2015. In fact, most of my working hours was spent with them: getting frustrated with each other, managing this frustration, and simply having fun. I hope that they had as much fun as I did, and I would like to honor their participation, as I would have nothing to present without their kind help. Therefore, in an alphabetical order, I would like to thank Dolittle, Dunja, Figaro, Fini, Heidi, Juno, Kiwi, Konrad, Linda, Maggan, Manda, Mayday, Moneypenny, Muki, Muppet, Naong, None, Pipin, Rickard, Rugga, Tosta, Santino, Selma, Siden, Utara, Zozo. I would also like to thank twenty-six people who contributed a lot of effort, trust and time to bizarre tasks described in this thesis. Although they must remain anonymous, I am grateful to every single one of them.

Moreover, I would like to acknowledge my colleagues in and around the Cognitive Zoology Group: Ivo Jacobs, Can Kabadayi, Claudia Zeiträg, Kristin Osk Ingvarsdottir, Andrey Anikin and Stephan Alexander Reber. I thank Ivo for his critical and valuable feedback. I thank Can for our cooperation on one of the manuscripts outside of this thesis, his friendliness and warmth. I thank Claudia for a breath of fresh air, her feedback and great time that we shared in the past few months. I thank Kristin for a great atmosphere in the office, her statistical tips and feedback. Finally, I thank Andrey for his help with some statistical questions.

I would also like to thank Fanni Faegersten, Carina Holmberg Pousette and Anders Ruland for their time and help in my last year of studies. Without Fanni and Carina, I would not be able to explore non-academic workplaces that match my interests. And without Anders, I would not be able to realize and believe in a project that could potentially change many more animal lives than I could ever change inside the academia.

Furthermore, I am thankful to my colleagues at Lund University Cognitive Science: Betty Tärning, Trond Arild Tjøstheim, Christian Balkenius, Kerstin Gidlöf, Annika Wallin, Petter Johansson, Gabriel Vogel, Jana Holsanova, Zahra Gharaee, Agneta Gulz, Magnus Haake, Birger Johansson, Peter Gardenförs, Jens Nirme, Thomas Strandberg and Eva Sjöstrand. I am especially thankful to Betty and Trond for their kindness and help, and to Kerstin for her valuable suggestions.

I thank Joost van der Weijer, for his statistical and technical support, and Anton Wrisberg, for his help with the memory study with great apes. I am very grateful for a chance of working with Helena Kelber, Marcus Lindblom Lovén, Felicia Lindström, Brigitta Nagy, Johan Sahlström, Klara Thorstensson and Therese Wikström, who all put more effort and time into our collaboration than Elia and I could ever ask. I also thank editors and reviewers, thanks to whom I learnt a lot and improved the manuscripts included in this thesis.

I would like to acknowledge all funding agencies that supported my work, both through grants awarded to Mathias Osvath and to myself. Therefore, I thank Swedish Research Council, the European Commission, the Polish Ministry of Science and Higher Education, Stiftelsen Roy och Maj Franzéns fond, Knut och Alice Wallenbergs stiftelse, Fil dr Uno Otterstedts fond för främjande av vetenskaplig undervisning och forskning, and Kungliga Fysiografiska Sällskapet i Lund.

Last but not least, I am forever grateful to my family who raised me to be the person that I am today. I am especially thankful that they have never set up limits in my mind as to whom I could be and what I could do with my life. I hope that I made them proud and that, at least to some extent, my work allowed them to develop more satisfying bonds with animals in their lives. On this note, I would like to thank Dilmah, Filemon, Ina, Penny, Timmy, Snow and Stefan for their kind presence in my everyday life.

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Overview of the thesis

This thesis was driven by a keen interest in testing memory without words, and a passion for working with animals. These two driving forces resulted in new experimental setups that were tested with five animal species: the common raven *(Corvus corax)*, the Goffin's cockatoo *(Cacatua goffiniana),* the Sumatran orangutan *(Pongo abelii),* the common chimpanzee *(Pan troglodytes)* and the human *(Homo sapiens sapiens)*. Although from the biological point of view, humans are animals, just like the other four species, they will be referred to as *humans* or *people*, and the other animals will be referred to as *animals* throughout this thesis for the sake of convenience.

In this thesis, I compared some aspects of attention, working and long-term memory across the five species. All these species have something in common: on the one hand, they have well-developed senses that allow for acquiring rich and detailed information about the environment, and on the other, they also have specialized body parts that allow for acting on this information. But between these two steps – acquiring the information and acting upon it – this information must be selected, processed and prioritised, and this is where the processes of attention, working and long-term memory pitch in.

Having well-developed senses and specialized body parts is a blessing and a curse. It allows for rapid and accurate responses to a dynamically changing environment, but vastly complicates everyday life; all of sudden, the continuous dynamic changes in the environment are revealed, and call for action. The everyday life becomes a streak of complex concurrent problems that require rapid solutions. As all problems cannot be resolved at once and conflict with one another, they could turn into a never-ending cognitive pandemonium, if it was not for efficient information processing capacities. Navigating in the continuous flow of information is all about resolving the conflicts by sorting, selecting, and prioritising at all steps of information processing – from acquiring the perceptual information, through comparing it with the records stored in memory, to issuing the accurate behavioural response.

In this thesis, I argue that harnessing the flow of information is what memory has evolved for. Memory allows for resolving conflicts that pervade everyday life of the five tested species. The capacity for conflict resolution is an inherent part of attention, working and long-term memory. This is true both for immediate contexts, when one needs to sort, select and prioritise the information that is currently available in the environment, and for delayed contexts, when one needs to sort, select and prioritise the information that was available in the past and is now retrieved from memory.

Attention, working and long-term memory are certainly available to the five tested species, but it is unclear how each species uses these capacities. In principle, this question could be split into four sub-questions: (1) how do these capacities develop from birth to adulthood in each species? (2) which mechanisms support these capacities? (3) how may they have evolved? and finally, (4) what purpose do they serve in everyday life of each of the tested species? (Tinbergen, 1963). However, giving an answer to all these sub-questions is impossible at this point in time, and certainly would take more than a lifetime of continuous research. For this reason, in this thesis, I focus on two of the four questions: of evolutionary function, and of mechanisms that may support the capacities of attention, working and long-term memory. To answer these two questions, I bring together some ideas developed and discussed in several fields of research, such as psychology, animal cognition and computer modelling. The introduction to the thesis is a critical collection of those ideas that situates the thesis within the previous research and lays out the theoretical background of the experimental setups tested within the scope of this thesis, and inspired by the issues and findings discussed in the introduction.

In the first and the second part of the introduction, I argue that long-term memory has evolved for problem solving, and that mechanisms of long-term memory have evolved under the pressures of dynamically changing environments. Under these circumstances, not only attention and working, but also long-term memory had to allow for rapid and flexible responses rather than for collecting a perfectly accurate picture of what happened in the past. Therefore, I argue that favouring flexibility over accuracy may have been built into human long-term memory. This built-in support for flexibility over accuracy in long-term memory may have driven impressive human adaptation to the ever-changing environment. If this assumption - that a demand of flexible adaptation to the ever-changing environment drove the evolution of long-term memory - is correct, a shift in thinking about animal memory may be justified.

In the third part of the introduction, I discuss various findings from animal memory research, many of which were generated in response to a shift in human memory research that occurred in the 1980s. Since that shift, some aspects of long-term memory have been considered uniquely human (Tulving, 1985), and a lot of effort in comparative behavioural research was put into challenging this hypothesis (e.g., Clayton & Dickinson, 1997). In the third part of the introduction, I discuss some of these efforts, as wells as other relevant aspects of the current state of knowledge on animal memory. I conclude that all aspects of memory – from attention to long-term memory – may be attuned to resolving complex and problematic situations, which are a ubiquitous challenge in ever-changing environments. Therefore, focusing animal memory research on the function of memory, and memory flexibility, might be a good way of moving forward and finding out how memory of different animal species actually works.

The third part is followed by the fourth, with some theoretical considerations behind cross-species comparisons of cognitive capacities, and by the fifth, with a brief overview of the papers included in this thesis.

A considerable part of the introduction is built around studies with humans, but I do not support the anthropocentric approach to comparative behavioural studies (cf. Emery, 2017). I have no interest in whether animals do what humans do, when given a similar cognitive task. Whenever animals and humans are tested in analogical experimental setups here, the performance of humans is of interest only because human memory is far better studied than animals'. None of the experimental setups introduced in this thesis were tested before, so it was unclear whether they tapped into the desired aspects of memory. Giving the task to humans allowed for comparing their scores on the new task with the established scores in other, extensively tested tasks, that have previously been shown to tap into the desired aspect of memory.

The main goal was to find out how different species respond to comparable experimental setups, and to give as equal opportunities as possible to the individuals within each species. Therefore, I adjusted the experimental setups to the sensorimotor skills of each species, and attempted to minimize the effect of individual variation in such skills on the performance in the task. For instance, regardless of how the individual animal was handling the tool – whether with a beak and a leg, or with the beak only – or how long it took for the individual animal to solve the problem – whether it was slightly afraid of the apparatus and took more time to approach it, or immediately explored it - the individuals within each species were given as equal chances of succeeding as possible.

Just like biologists tend to investigate how different animal species solve certain environmental challenges with their bodies, I investigated how different animal species solved certain problems with their cognitive capacities. "Different species have evolved to solve problems of survival that are unique to them" (Schacter & Tulving, 1994; p. 30), but, for the five tested species, these problems might have been similar enough to drive similar memory capacities.

Part 1. What is memory for?

Memory in every-day life

Making coffee with an unknown espresso machine, we are reminded of familiar espresso machines, even if we have not used them in years. Entering a rental car, we are reminded of our own, and seconds after sinking into the seat, we are ready to drive off, nervously but usually without scratching the car. Our current situation always reminds us of another past experience or experiences because it partially overlaps with them. Our past informs our present behaviour on a daily basis. Because we have access to memories, we are rarely helpless in new situations.

We access and retrieve memories so swiftly that we seldom notice our constant dependence on memory retrieval. Although most of the time we retrieve past situations automatically, we can also travel back in our minds to the original situation and then apply its consequences to the current context. This ability, called *mental time travelling* (Tulving, 1985; Suddendorf & Corballis, 1997), has been extensively (and fiercely) discussed in the last two decades, and we will come back to this issue in the second part of this introduction. In the meantime, let us consider another property of our memories. In order for the memories to be stored and retrieved, our experiences need to be encoded, and there are two different ways in which we do it: first, we scan our surroundings and encode some of their features without paying attention; second, once something changes in the surroundings and draws our attention, we can concentrate on it and make sure that we remember it. This means that we can keep track of the surroundings without concentrating on anything particular (Kanerva, 1988). We, by default, continuously scan the external world for sensory information and compare it with our internal model of the world, that is with “how things were up to now” (Kanerva, 1988). Thanks to the constant influx of sensory information (Gibson, 1966), we can build and update the internal model of the world, and use it in future situations.

We will soon need to agree on a set of terms that will be used throughout this introduction because without it we will easily confuse memories with experiences, experiences with situations etc. I will do so in *Terminology*, but for now, let us consider how we use our memories in everyday life. We do not need a perfect match between features of the current situation and the past one. As long as some of these features overlap, we can detect this overlap and match the two situations. This means that we can operate on incomplete information, so we do not even need our memory of the past to be perfectly accurate: as long as we can extract and use relevant features of the past situation in the current context, the irrelevant features can even be inaccurately remembered. It does not affect our performance in the current situation. All that matters is detecting and matching of the relevant overlapping features: it allows us to resolve never-encountered situations because they share some relevant features with past situations.

Memory systems

Thanks to the ability of matching the overlapping features across situations, we are ready for a multitude of situations which we have never encountered, and which may never come. But if they do, we will be able to react rapidly, almost as if we have already encountered them. It will be possible not because our memories are perfectly accurate; but because we can use our memories in a flexible manner. Before we move any further, we need to realize that, whenever we use past situations to inform our behaviour here and now, we employ the long-term memory system. Long-term memories can pertain, for instance, to data- or rule-based information (Cohen, Eichenbaum, Deacedo, & Corkin, 1985). Accordingly, two separate and distinct systems handle such memories: a declarative system deals with our memories for data-based information, e.g., facts and a procedural system deals with our memories for rule-based information, e.g., motor skills (Cohen & Squire, 1980).

In this introduction, we will be particularly interested in the declarative system, which deals with "knowing that" something happened in the past. But we could know that something happened from two distinct sources: either we witnessed it happening, as a mere observer or as a participant, or we were informed that something had happened: someone told us or we read about it in the newspaper. Witnessing something adds a personal aspect to the knowledge, which hearing about/reading about does not add. Therefore, a distinction between these two types of declarative knowledge is necessary, if one wants to investigate memory processes behind them and communicate with others. To facilitate communication among memory researchers in the 1970s and all years to come, Endel Tulving (1972) introduced two further terms: of a semantic memory system and of an episodic memory system. Although initially these terms signified two complementary information processing systems that were neither structurally nor functionally separate, such separations have been repeatedly shown in psychological research since the introduction of the terms (e.g., O'Reilly, Bhattacharyya, Howard, & Ketz, 2011). With such structural and functional separation come differences in system-specific content (what is stored), encoding (how it is written into memory) and retrieval (how it is used in the future). The semantic memory system is prerequisite for using language and handles structures of concepts. The episodic memory system, on the other hand, operates on personal experience; it records a non-objective version of events which, by temporal and spatial relations, are connected to past, simultaneous and potential future situations. Because in this introduction we are interested in how our past informs our present and our future, we will focus on the episodic memory system, especially on its content, ways of retrieval, and function.

Terminology

The content of episodic memory is experience-near rather than a precise recording of the past situation (Conway, 2008). Therefore, already at the stage of encoding, our experience and, thereby, our record of the situation is not perfectly accurate. From now on, let us distinguish our "*experience*" from "*a situation*". *A situation* is something that happens in the external world. As witnesses and/or participants, we perceive this situation in a certain way, and sensory information that we obtained in the situation will be called our *experience. A record* will signify a sequence of information that represents an experience (Kanerva, 1988, p. 1), which can be encoded, stored and retrieved in the future. This term, *a record,* could be also substituted by *a representation*, but *a representation* can have different meanings in computer modelling (e.g., Rumelhart & Norman, 1983), psychology (e.g., James, 1980; Malcolm, 1970) and philosophy (e.g., Pitt, 2018), so using this term could potentially confuse some readers. We will use *a record* instead. Records are stored in our memory, and according to different accounts, can be either stored in single locations (localized memory models), or can be distributed over multiple locations (distributed memory models; Kanerva, 1988, p. 11) in memory. Because distributed models of memory are faster than the localized models and require a simple centralized executive system (similar to our prefrontal cortex or ravens' nidopallium caudolaterale, they are perhaps a more accurate model of how human (and animal) memory works. Distributing a record over multiple locations creates multiple *traces*, which are parts of the record. In other words, the record is split into several traces, which are then stored in different locations. This means that a single location can contain traces that belong to different records.

We have already established that we can use our records of past situations to respond to the current situation. This means that something in the current situation can act as a *cue* that triggers retrieval of different *traces* of our records. For it to be possible, the cue and the trace must have something in common. As mentioned above, we can exploit the overlap in the features of the current and the past experiences, that is these features that are shared by the cue and the trace. Because it is difficult to operationalise such features, we will use the term of *a pattern.* A pattern will signify a sequence of information (features) that is shared by the cue and the trace.

To put less effort into deciphering the rest of this introduction, let us recapitulate the introduced terms. We can encode and store a record of our experience of a past situation. To do so as efficiently as possible, the record is split into traces which are stored in different locations. The traces contain familiar patterns (sequences of information) so that when we encounter a cue - an unfamiliar but partially overlapping pattern – we can retrieve the traces and get information on our (un)successful behaviours in the retrieved past situation or situations.

These terms – *records*, *cues* and *patterns* are, to some extent, based on Pentti Kanerva's account of sparse distributed memory (1988), which will be more extensively described in the second part of this introduction. Because numerous accounts of memory have been offered in the past and we will use several as we move forward, two problems could potentially emerge. First, some of the terms will be used by several accounts, but they will carry different meanings. Second, even when the accounts will address the same or similar memory processes, they will sometimes employ different terminologies and often disregard distinctions, e.g. between memory systems, introduced within other accounts. For instance, in two computer-modelling accounts that we will use, first put forward by Pentti Kanerva (sparse distributed memory; 1988), and second put forward by Boicho Kokinov (associated memory-based reasoning; 1988a, 1988b), we will not find the familiar distinction between declarative and procedural memory system. Neither of these models contests the existence of such distinction in human memory; but they simply choose a holistic approach to our experience, which rarely consists of purely data-based or rule-based information. Because both models predict how we will use our past experiences in a future situation, they operate predominantly on episodic memory system. According to Endel Tulving's definition, episodic memory system records a non-objective version of situations which, by temporal and spatial relations, are connected to past, simultaneous and potential future situations (1972). Therefore, even if Kanerva and Kokinov are not explicitly interested in this particular system, they are essentially modelling how the episodic memory system may work.

To figure out how the episodic memory system works, we can use evidence generated within several research fields, such as psychology, computer modelling and – to a lesser extent – comparative behavioural studies. This means that computer models, verbal reports, neuroimaging of brain activity, and human and animal behaviour can all provide us with clues on how the episodic memory system works. In fact, an abundance of data has been accumulated within each field over the years, and it would be impossible here (if it is possible at all) to bring all the data together, thoroughly discuss and arrive at some new methods of studying episodic memory in animals. Because inventing and implementing such methods, and not a review of everything related to episodic memory, is the ultimate goal of this thesis, we have to approach it in another way. The challenge of finding this new approach is essentially the same as any unexpected situation that we need to resolve in our everyday life. We already know that we can search for and retrieve relevant traces from different records in response to a somewhat overlapping cue. We will apply the same method in this introduction: we will use some evidence generated within the three fields of research – psychology, computer modelling and comparative behavioural studies – to figure out (1) how we remember, (2) what makes it possible for us to remember in this way, and why it is relevant for animal memory research, (3) how animal memory was previously tested and what was found in these tests, (4) why would we compare different species in studies of memory, and finally, (5) what happened in some actual studies with great apes, Goffin's cockatoos, ravens and people (part 5).

Memory malfunctions

Before moving on to the next parts of this introduction, let us consider the following question: how accurate is our episodic memory? I have already mentioned that the content of episodic memory is a record of our experience, not a precise recording of the situation (Conway, 2008). This is the first problem which might lead to a somewhat inaccurate account of the past situation when we, for instance, confront it with other witnesses or participants who were present in that situation. Further, we are sensitive to similarities between patterns of cues and traces, which allows us to adequately react to new situations. But this sensitivity to similarities may be a double-edged sword; already in 1972, when Endel Tulving proposed his first definition of the episodic memory system, he suggested that records encoded, stored and retrieved from episodic memory could be prone to involuntary transformation and loss of information (1972). This suggestion has been supported by several studies of memory malfunctions in the last decades. Some of these malfunctions have grave consequences, when, for instance, innocent individuals are mistakenly identified and convicted based on eyewitness reports (Hope & Sauer, 2014). But many of these malfunctions blend into our everyday experiences and often go unnoticed.

Because the records are split into traces, we need to put them back together if we want to retrieve the recorded experience of the past situation. The traces contain information on what sensory information was obtained in the situation, how it was evaluated and interpreted, and what actions were undertaken to resolve the situation (Johnson & Chalfonte 1994; Metcalfe, 1990; Moscovitch 1994; Schacter, 1989; Schacter, Norman, & Koutstaal1998). We retrieve the experience from the traces, whenever the pattern in the cue overlaps with the pattern stored somewhere in these traces. The retrieval of the pattern in the trace is triggered by the pattern in a retrieval cue, and leads to a process called *pattern completion* (McClelland, 1995). Upon the cue, a subset of the most overlapping traces is reactivated. Each of these traces may belong to different records of the past experiences. As mentioned above, traces belonging to the same record are distributed across different locations in memory, and so once the most overlapping traces are reactivated, the activation spreads to other traces that originally belonged to the same record.

A memory system that operates in this way must solve several problems to generate mostly reliable records of the past experiences. These problems can occur either at encoding or at retrieval of records. For instance, at encoding, the system can produce so-called source memory failures. In source memory failures we cannot retrieve a complete record from the available traces, which means that our memory system failed either of two challenges. The first challenge occurs when a record of the experience is formed: traces that belong to the same record must be linked together to form a coherent account of what happened in the past (Moscovitch, 1994; Schacter, 1989). If this fails, we will retrieve only fragments of sought-after records in the future. The second challenge occurs because a record must be sufficiently separated from other records, that is traces of one record must be sufficiently separated from traces of another record. This is where *pattern separation* must be employed (McClelland, 1995). If two records are not sufficiently separated, we will not be able to fully retrieve each of the records. But a failure in pattern separation can also lead to another error; when records extensively overlap with each other, we may recall the general similarities (Hintzman & Curran, 1994) or gist (Reyna & Brainerd, 1995) shared by the records, but fail to retrieve traces that distinguished the records from each other (Schacter et al., 1998)

As we already know, at retrieval the pattern in the cue is matched with the pattern in the trace (or traces). But this is only the first step on our way to retrieving the complete record. Once we find an overlapping trace, we need to determine whether the trace belongs to a record of something that has actually happened (Johnson, Hashtroudi, & Lindsay, 1993). To do so, we set up certain criteria, and if the trace meets these criteria, we will accept it as reliable. Next, we need to determine if the trace belongs to a sought-after record, and then implement a solution found in this record. But at retrieval we also risk various memory failures. For instance, we can retrieve a matching, but an irrelevant record that will not help us resolve the present situation, if retrieval cues match traces belonging both to the relevant record and some irrelevant ones (Nystrom & McClelland, 1992). Furthermore, sometimes information present in the retrieval cue can overshadow information present in the target trace, and alter our report of the past situation (Schacter et al., 1998). For instance, in so-called schema-driven recall errors we can generate inaccurate accounts of past situations because we can produce and use a cue that, alongside sensory information obtained in the present situation, contains often used and easily accessible schematic knowledge (Bahrick, 1996). In such case, asked what happened in a given situation, we might rely on knowledge of what usually happens under similar circumstances instead of retrieving that concrete situation. Most of the time using easily accessible schemas will be much faster than retrieving a concrete past situation; but it can also hinder retrieval of a better solution from the sought-after record.

Mechanisms of retrieval and their consequences will be described in greater detail in part two of this introduction, after I have described what allows our memory to work as it works. So far, we learned that memory is prone to several involuntary malfunctions that often evade our perception. Most of the time memory is not perfectly accurate, but accurate just enough for us to rely on it in everyday situations.

Adaptation

Would we be better off without these memory malfunctions? The answer is “no”. The same processes that allow us to retrieve records in a fast, efficient and flexible way are the ones responsible for these malfunctions (Schacter, Guerin, & Jacques, 2011). Simply put, such malfunctions reveal ingenious adaptations to demands of a fast and unpredictable world. Even if we could ever achieve perfect memory accuracy, achieving it would make our behaviour slow and rigid. We would not only fail to keep up with the ever-changing environment – we would be completely helpless in the face of never-encountered situations. But, as a product of evolution, our memory must be a well-adapted tool – perhaps accuracy is just not what memory has evolved for. If accuracy is sometimes sacrificed for the sake of flexibility, flexibility must be a key function of our memory. In practice this means that some cognitive processes have a twofold function: they speed up memory processing and responding to new situations, but sometimes produce memory distortions. This adaptive account of memory distortion has gained a lot of attention and support in the recent years (e.g., Boyer, 2009; Howe & Debrish, 2010; Newman & Lindsay, 2009; Schacter & Addis, 2007; Sutton 2009; Otgaar, Howe, Smeets, Raymaekers, & Beers, 2014).

Memory has been subject to selective pressures throughout human and animal evolutionary history (Murray et al., 2016); memory always depends on neural structures which, like all biological structures, evolved over time to support adaptation to environmental demands. The more complex these demands become, the more complex the neural structures must become, if they are to support an adaptive memory system (e.g., Gregory, 2008). Likewise, our episodic memory is supported by networks of brain structures whose activation can be investigated with various neuroimaging techniques. Thanks to such techniques, a core brain network that supports episodic memory retrieval has been identified (e.g., Schacter, Addis, & Buckner, 2007). This core system involves medial prefrontal and medial parietal areas, medial temporal lobe (including hippocampus), as well as lateral temporal and lateral parietal areas (Buckner, Andrews-Hanna, & Schacter., 2008; Schacter et al., 2007; Spreng, Mar, & Kim, 2009).

Now, under certain circumstances, neuroimaging of activation spreading across this network can provide support in favour of the adaptive account of memory: some memory malfunctions are produced by the same areas that are, at least most of the time, responsible for adequate behaviours. This is what happens, for instance, in above-mentioned schema-driven recall errors. These errors are predicted by activity in the medial prefrontal cortex and lateral parietal cortex – two areas that are also responsible for so-called contextual processing (Aminoff, Schacter, & Bar, 2008; Schacter et al., 2011). When items typically co-occur with one another in a specific context, we classify them as such; and if we encounter one of the objects in this context in the future, we will automatically assume that the other item will occur in it as well. Remembering and operating on such contextual associations helps us organize the external world and allows for predicting what will likely happen next in specific contexts (Bar and Aminoff, 2003). Because a lot of repeatedly encountered situations fit well into such schemas, the assumptions save us time and energy, which is crucial for efficient functioning in the ever-changing world. But this very mode of operation also leads to errors whenever a seemingly familiar context contains only some, but not other usually co-occurring items. This adaptive cognitive process – of complementing sensory information with schematic knowledge – can lead to inaccurate retrieval of a record of our past experience because we tend to falsely recognize items which have never been a part of the record, but are only contextually associated with items that have (e.g., Gallo, 2006).

Susceptibility to so-called associative memory errors is what makes us better at convergent thinking, that is the ability to generate broad and numerous associations (Dewhurst, Thorley, Hammond, & Ormerod, 2011). Simply put, the more creative we are, the more we are prone to associative memory errors. Such errors also reflect an operation of a healthy memory system; they are reduced in patients with amnesic syndromes after damage to the medial temporal lobes, but this reduction comes with a considerable memory impairment (review in Schacter, Verfaellie, & Koutstaal, 2002). The damage to the medial temporal lobes also lowers susceptibility to so-called gist-based errors. They arise from a malfunction of gist-based processes which normally support generalization and abstraction (Brainerd & Reyna, 2005; Schacter, 2001; Gallo, 2006), that is transferring responses onto situations somewhat similar to stored experiences. Because of these gist-based processes, we tend to falsely recognize items which have never been a part of the record, but are only perceptually or contextually similar to items that have. Again, neural areas that are activated during false recognition, including the prefrontal cortex, the parietal cortex, and the medial temporal lobe (Garoff-Eaton, Slotnick, & Schacter, 2006) overlap with the areas activated during generalizing and abstracting.

In the face of a new situation, we can rely on records of actual experiences stored in our memory. However, we can expand our pool of available records by imagining what may happen in the future, and how we may react to potentially upcoming situations. This ability allows us to retrieve and flexibly recombine already existing records to simulate alternative future scenarios without engaging in actual behaviours (Schacter & Addis, 2007). But because both imagining and remembering recruit the same components of the core network (Addis, Pan, Vu, Laiser, & Schacter, 2009), including the medial prefrontal cortex and the hippocampus, sometimes traces of actual and imagined experiences can be miscombined into inaccurate records (Newman & Lindsay, 2009). Just like in gist-based errors, the imagined experiences, which share perceptual or conceptual features with actual experiences, are most likely to affect the actual records.

To sum up, several cognitive processes that support an efficient and flexible use of memory, are sometimes overtly sensitive to irrelevant similarities between otherwise unrelated experiences. In unrelated experiences, perceptual and/or conceptual similarities between two situations cannot inform our behaviour: a solution that we applied in a past situation will not help us resolve the present one. But most of the time, being sensitive to, matching and exploiting such similarities is arguably the most adaptive way of dealing with rapid and unpredictable environments.

Part 2. Which mechanisms support a flexible memory system?

Access

When we step out of a train in an unfamiliar town to set out for a booked hotel, we encode a sequence of images that begins with a view of the platform and ends with a view of the hotel facade. This sequence contains numerous items that we encounter on our way. Now, should we, during our stay, stumble upon a tourist who would show us a photo of an allegedly noteworthy landmark, asking if we have seen it in the area, we could immediately give an answer. Sometimes it will be a definite yes or a definite no, and sometimes we will only be able to take a guess. We can give any of these answers without scanning records of our walk from the platform to the hotel. This shows that we can randomly access our records of past experiences. On the last day of our stay, to catch a train home, we would need to take a walk again; this time from the hotel to the station. But here our memory would fail us if we could access the record only in a random manner. Thankfully, we can also retrieve past experiences sequentially – remember what happened after we left the platform; that we turned left to the park, then right to the market and so on, until we saw the hotel facade. All we need to do is follow a reversed version of this sequence, and get back to the station.

To model how our memory works, one needs to take these two ways of retrieval into account: that we can retrieve items both at random and in sequence (Kanerva, 1988; p. 13). This is a premise behind a sparse distributed model of memory which was put forward by Pentti Kanerva in 1984. Why would his model, and not others', be relevant for this introduction? First, the sparse distributed model reliably predicted phenomena documented years after its initial publication, as it accounts for all of the above-mentioned memory malfunctions. Second, it is built on simple premises that do not require any uniquely human memory capacities, which means that the model allows for evolutionary continuity within memory capacities. Third and most importantly, it was successfully used to model cognitive processing behind complex behaviours without reliance on complex computation (Kleyko, Osipov, Senior, Khan, & Sekercioglu, 2016). For instance, the model was recently used in so-called Vector Symbolic Architectures and building an artificial learning system that imitated concept learning in bees (Kleyko, Osipov, Gayler, Khan, & Dyer, 2015). As this modelling technique can be applied to any processing that involves focusing on a limited number of objects at a time, it could in principle be used to model complex cognitive capacities, such as mental time travelling. This is what boosts the predictive value of this model and sets it apart from others: it is versatile enough to accommodate various memory phenomena and grounded enough to generate verifiable hypotheses on how animal memory could work. Because suggesting and implementing new methods of measuring animal memory is the ultimate goal of this thesis, the sparse distributed model is the best fit for the job.

The sparse distributed model operates on patterns expressed in long vectors of bits. We already know that patterns are important for encoding and retrieval of records, and that remembering relies on matching patterns in the cues and in the traces. The patterns – both familiar (in the traces and already-encountered cues) and unfamiliar (in never-encountered cues) – serve as *addresses* to memory. The memory has an autonomous addressing framework within which traces are stored and retrieved from the addressed locations in the memory. Addressing the memory does not need to be exact; that is, searching for a stored pattern with an address only similar to the pattern's original storage address will still end in the pattern's successful retrieval (for further details see Kanerva, 1988; p. 98). This means that to read from the memory, we do not need to know the exact address pattern that was used in writing the trace into the memory. We are simply sensitive to similarity between the *read* and the *write* address. But when many similar patterns have been used as *write* addresses, individual patterns stored under each of these addresses cannot be recalled exactly. I have already described this problem in slightly different terms as a failure in pattern separation that allows for recovering only the general similarities (Hintzman & Curran, 1994) or gist (Reyna & Brainerd, 1995) shared by the records of our past experiences. This failure is accommodated by the sparse distributed model, which in such cases would, instead of individual patterns stored under many similar *write* addresses, recover only a statistical average of these patterns. This shows that the tradeoff between speed and accuracy is at the very core of the model: storing patterns under many similar addresses means that activation can spread faster, but by default blurs the accurate picture of individual initial records.

The internal model

Remembering relies on matching the patterns present in the cues with those stored in the traces. And that the cues can comprise not only of incoming sensory information sought by our perceptual systems (Gibson, 1966), but also some other information with which we complete the sensory input without voluntary control.

This means that the cue is not a pure reflection of the influx of information from external world; we construct the pattern in the cue through meshing the sensory input with the internal model of the world. Developing such an internal model does not happen overnight; it is constantly shaped in encounters with the external world. When individuals, both animals and humans, interact with the external world, they learn to deal with it in increasingly efficient ways. They accumulate records of previous experiences to make predictions about the future encounters. This principle applies not only to episodic or declarative memory, but even to sensory perception: learning about the world often requires only repeated exposures to sensory information. Simply put, even sensory neurons can change their responses when, after behavioural response to a stimulus, the outcome of behaviour is not consistent with the expected outcome; that is, when an actual result of a given behaviour does not overlap with a predicted result (Guo, Ponvert, & Jaramillo, 2017). Thanks to this loop – predict, implement, update, and predict again – the individual can build the internal model of the world of the best predictive value.

Likewise, in the sparse distributed memory, the internal model of the world simply picks up statistical regularities in sensory information and uses these regularities to build up a dynamic model of the external world (e.g., Zacks & Swallow, 2007; Magliano, Radvansky, Forsythe, & Copeland, 2014). The world is what our senses report it to be (Kanerva, 1988, p. 99). But although the individual continuously builds and re-builds the internal model of the world, the act of building and re-building evades the individual's perception. The distinction between the internal and the external is only revealed when discrepancies between the internal and the external models occur. There is oneness to subjective experience; even though we construct the cues from sensory information (the external world) and, for instance, schematic knowledge (the internal model of the world), we perceive the cues as one. Most of the time we can estimate how much of our experience comes from the internal model and how much from the external world because the subjective quality differs for the experiences mediated by the senses and for the experiences produced by the internal world based on records stored in memory. This means that we are usually able to tell whether something has actually happened or whether we have only imagined it happening. And, as we already know, imagining possible experiences mediated by the internal model of the world allows us to predict (model) possible future situations, simulate our potential behavioural responses and consider their outcomes (e.g., Hesslow, 2002). But sometimes the product of our imagination can be so rich in sensory detail that we will mistake it for something that has actually happened; and sometimes, as mentioned above, the imagined experiences can mesh with the actual experiences as long as they have enough perceptual and/or conceptual features in common.

Learning

How could this work in practice? In the sparse distributed model, the individual's sensory information at a moment is expressed in a long vector of bits; this vector consists of patterns that represent features of perceived items. A sequence of such vectors will represent the passage of time. As mentioned above, memory operates well on such sequences when matching and retrieving patterns, so it can naturally deal with them at any moment. Because information from the senses and information from the memory mesh seamlessly together and appear as one in the subjective experience, both the senses and the memory must feed into a certain part of the model's architecture, which is responsible for this meshing. In the sparse distributed model this part is called the *focus*, and so the subjective experience about the world is represented by a *sequence of patterns in the focus*. The patterns within the focus can be stored as *data* in memory once they leave the focus, but can also be used as *addresses* to stored memories. When the present situation resembles a past one, a sequence created by the senses in the focus resembles a stored sequence. And when the sequence in the focus is used to address the stored sequence, it retrieves what happened in the past situation. The retrieved information is then compared with what is happening now, and used as a criterion for updating the internal model of the world (Kanerva, 1988, p. 101).

However, the updating of the internal model would be of no use, if the individual could not act on the newly acquired information. Therefore, to adapt to the incoming versions of the world, the individual must be able to act, that is implement motor responses; and to implement motor responses and learn from their outcome, the individual must be able to model own actions. Memory does not only contain information about items and their features; it also contains information which behaviours were desirable and which were undesirable in response to these features. The sparse distributed model makes an empirically derived assumption that individuals have built-in preferences and dislikes; some outcomes are desirable and others are not. The individual has also an access to some instinctive responses (ways to act) which have been acquired over evolutionary history of the species, and so available to the individual without any learning. The responses, that is action sequences, that lead to desirable or undesirable outcomes can be likewise called desirable or undesirable. Because the sparse distributed model accounts not only for acquisition of sensory information, but also learning of actions, it can explain the mechanisms behind both simple, slower and more rigid ways of learning e.g., by trial and error, and complex, faster and more flexible ways, e.g., learning in social settings (for details see Kanerva, 1988). That the model accommodates both perceptual and motor learning, increases the model's predictive value of how memory works. It reveals a principle that perhaps pervades all systems involved in behavioural responses – from sensory perception (Guo et al., 2017), through memory, to action. This principle, identified here as a tradeoff between accuracy and flexibility, and favouring flexibility over accuracy, perhaps also applies to episodic memory, as has been already supported by above-mentioned findings from psychology. Thinking about episodic memory as a complex proxy of behavioural flexibility is perhaps more potent for generating tests of the animal versions of episodic memory than focusing on its predominantly verbal expressions in humans (contrary to e.g., Tulving, 2002; Mahr & Csibra, 2018; in accordance with e.g., Berntsen, 2018). The consummate behavioural flexibility observed in humans is most likely driven by human episodic memory, and benefits from verbal processing, but these two observations alone tell us little about the animal episodic memory. We will return to this issue in part 3, when reporting what is thought and what is known about the animal versions of episodic memory. First, however, let us have a closer look at mechanisms of updating the internal model of the world through episodic memory, revealed by years of studies with humans and a recent study with rats.

Updating

We can encode, store and retrieve the records of our past experiences from episodic memory. We store them in portions – traces – and putting these portions together is a dynamic process, in which we sometimes retrieve only an averaged and incomplete version of what has actually happened. But our episodic memory system can do more than that – it dynamically matches and incorporates newly acquired patterns alongside the stored ones to rapidly update the internal model of the world (e.g., Edelson, Sharot, Dolan, & Dudai, 2011). This ability is perhaps supported by the medial temporal lobe and the prefrontal cortex as these brain areas are both activated in encoding of memories (Okado & Stark, 2005; Baym & Gonsalves, 2010).

We have already learned that having an access to records of previous experiences allows us to make predictions about upcoming situations, for instance, about outcomes of our behaviour. This ability, of making predictions from stored information, has been recently considered a general coding strategy (Bar 2007; 2009; Ouden, Friston, Daw, McIntosh, & Stephan, 2012) and a prominent function of a "predictive brain" (Bubic, Cramon, & Schubotz, 2010; Clark, 2013; Dudai, 2009; Friston, 2012; Hohwy, 2013; Koster-Hale & Saxe, 2013). But making relevant predictions requires relevant records; and having relevant records requires a mechanism that would allow for maintaining the records' relevance. To understand how this mechanism works, we need to understand three processes that support it: memory consolidation, memory reactivation and memory reconsolidation.

For some period after acquiring a record of new experience, the newly acquired record is labile and vulnerable to alteration (Hardt, Einsarsson, & Nader, 2010). In this period, known as the *consolidation interval*, the record can be altered by inducing amnesia (Duncan, 1949; Flexner, 1965), introducing a new competing experience (Gordon & Spear, 1973) or some enhancing procedures (McGaugh & Krivanek, 1970). After a delay, that is outside of the consolidation interval, these manipulations are no longer effective because the traces have already been consolidated, that is, stabilized and transferred from short-term to long-term memory storage. To illustrate how neural networks might deal with this task, a synaptic consolidation hypothesis was put forward more than half a century ago (Glickman, 1961; Hebb, 1949; McGaugh, 1966). According to this hypothesis, traces were captured in the brain through changes in synaptic efficacy which could take several hours. This process was supposed to be unidirectional: once the traces became stable and transformed into a long-lasting record, there was no way back. But this unidirectional character of consolidation was questioned at the beginning of the 1970s when several studies showed that even already stabilized traces can be altered – impaired, distorted or enhanced – under certain circumstances (Lewis 1979; Miller & Springer, 1974; Quartermain, McEwen, & Azmitia, 1970; Serota, 1971; Spear, 1973). Such alterations were considered possible thanks to memory reactivation. Reactivation reinstates the traces in their initial unstable, labile state which resembles the state of newly acquired traces in the consolidation interval (Gisquet-Verrier & Riccio, 2012). This means that the reactivated memory can also be impaired (Amorapanth, LeDoux, & Nader, 2000), distorted (Hupbach, Gomez, Bootzin, & Nadel, 2007; Walker, Brakefield, & Hobson, 2003) or enhanced (Lee, 2008), just like a newly acquired one. Reactivation can be triggered by both external and self-generated cues, and is prerequisite for any operation that changes or modifies the stored records. In the absence of external cues, no new information is added to the reactivated traces; this is when we observe a strengthening of these traces. But in the presence of the external cues, new information can be added to the reactivated traces, and this is when impairments and distortions of the traces can occur (Hardt et al., 2010). This means that cue-induced reactivation makes traces modifiable. When new information, recognized as relevant for the stored memory trace, appears in the environment, we can integrate this information into a preexisting trace (Gisquet-Verrier & Riccio, 2012). Therefore, the existing trace can be quickly updated by incorporating new information. Because such updating of traces presents an opportunity for their adaptive modification, it lies at the core of a predictive memory system in which the stored information should be as up-to-date as possible to generate accurate predictions about the external world. In other words, memory reactivation facilitates maintaining the predictive relevance of the stored traces (Lee, 2009), but induces memory malleability, again revealing an adaptation that favours memory flexibility over memory accuracy.

Record reactivation happens, for instance, when a need for updating of the stored record is recognized, that is, when a mismatch between a predicted and an actual input occurs. This mismatch, termed *prediction error*, drives the updating of already consolidated memories (Exton-McGuinness, Lee, & Reichelt., 2015; Fernandez, Boccia, & Pedreira, 2016; Pedreira, Perez-Cuesta, & Maldonado, 2004; Sevenster, Beckers, & Kindt, 2012; 2013; 2014). Because novel and/or surprising situations are in general better remembered than expected ones (Tulving, Markowitsch, Craik, Habib, & Houle, 1996; Habib, McIntosh, Wheeler, & Tulving, 2003), both novelty and surprise perhaps induce a violation of our expectations and, consequently, the prediction error. Situations are novel if they have never been experienced, and surprising if they differ from what we expected (Fernandez et al., 2016). Being sensitive to novelty and surprise can serve a potentially adaptive function of creating and updating records: we can detect what is new, and create a new, corresponding record; and we can detect what is surprising to update an existing but discrepant record, or create a new one.

Prediction error was initially found and investigated in the context of fear conditioning in laboratory animals, in which memories for stimulus-response contingencies were reactivated (Diaz-Mataix,, Ruiz Martinez, Schafe, LeDoux, & Doyere, 2013; Sevenster et al., 2012; 2013). However, it has been recently shown that it can also play a crucial role in reactivation of complex episodic memories (Sinclair & Barense 2018; Scully, Napper, & Hupbach, 2017), suggesting that both simple and complex memories can be reactivated. In nearly all studies that detected such effects, reactivation was investigated conjointly with reconsolidation. Reconsolidation, just like consolidation, is a time-dependent process, and happens within a certain time interval. It is necessary because after the traces are reactivated and their strength and/or content gets updated, they need to be restabilized before they can be stored in the long-term memory (Nader, 2000; Przybysławski & Sara, 1997; Sara, 2000). Memory reconsolidation has been extensively investigated and showed in many animal species (Dudai & Eisenberg, 2004; Lee, 2009; Schiller & Phelps, 2011). In fact, it has been first detected in laboratory rats treated with electroconvulsive shocks in the 1960s (Misanin, Miller, & Lewis, 1968), and, much later, with pharmacological manipulations (Nader, Schafe, & LeDoux, 2000). Since using electroconvulsive shocks hindered testing reconsolidation in human subjects, safe-enough pharmacological and behavioural manipulations were developed for this purpose in the 2000s (Brunet et al., 2008; Kindt, Soeter, & Vervliet, 2009; Schiller et al., 2010; Walker, Brakefield, Hobson, & Stickgold, 2003). Taken together, studies with animal and human subjects reveal that reactivation and reconsolidation pertain to a range of memories, from simpler, such as fear and appetitive, to more complex, such as procedural and declarative (Agren, 2014). Likewise, episodic memories – which are of a particular interest in this introduction – can also undergo reactivation and reconsolidation (Sinclair & Barense, 2018), and can be triggered by incomplete and/or surprising cues which are picked up by the hippocampus.

Interference

Consolidated memories can be reactivated, changed and reconsolidated. Reactivation makes them malleable which allows us to use an up-to-date memory system, but can also result in memory errors and intrusions which will limit our access to the original and correct version of the record in the future. We have already learned that we are sensitive to similarity; now we also know that we are sensitive to mismatches between the predicted and the actual. And paradoxically, susceptibility to both is driven by the hippocampus which, on the one hand, acts as a mismatch-novelty detector (Chen, Olsen, Preston, Clover, & Wagner, 2011; Kumaran & Maguire, 2007; 2009; Duncan, 2009; Lisman & Grace, 2005), but, on the other, acts as similarity detector, being responsible for already-mentioned pattern completion and pattern separation (Bakker, Kirwan, Miller, & Stark, 2008; Rolls, 2013). The hippocampus monitors the current perceptual input, compares it with the predicted outcomes, and generates a mismatch signal when prediction error occurs (Long, Lee, & Kuhl, 2016). Interestingly, the hippocampus is especially tuned to those unexpected outcomes that are similar to but slightly different from the initial prediction, that is, the outcomes that require detection of both similarity and dissimilarity.

The hippocampus needs to complete patterns in the cue, and compare the expected pattern sequences with the ones actually available in the perceptual input. But, as mentioned above, it can also engage in pattern separation to avoid extensive intermeshing between the stored traces. Specifically, it is involved in switching between encoding and retrieval of information to avoid overwriting, overlapping or excessive interference between similar, new and old, information (Gluck, Mercado, & Myers, 2013; Hasselmo 1994; Kumaran & Maguire, 2009; Lisman & Grace, 2005; Tubridy, 2011; Vinogradova, 2001). While *overwriting* and *overlapping* are self-explicatory terms, understanding *interference* may be less straightforward. So far, I was able to explain all memory processes without this term, but it is no longer possible.

Interference occurs when two records interact and influence each other, usually resulting in an impairment of one of them. In general, some records are more susceptible to interference than others, for instance, when they are acquired one after another, or when their traces contain similar patterns. In the first case, when records are acquired in close temporal proximity, there is a risk or retroactive and/or proactive interference. Interference is called retroactive when acquiring new information impairs a record of previously encoded information, and proactive when a record of previously encoded information affects acquiring a new information. But the term of *interference* is also used when traces that belong to different records overlap with each other, that is, when they contain similar patterns. Such interference is a by-product of pattern separation on the one hand, and, on the other, of the ability to retrieve traces in response to cues that contain only partially, and not fully overlapping patterns. Simply put, it is a by-product of the tension between separating and matching similar patterns, which both serve the same purpose - of fast and efficient encoding, storing and retrieving information - and both rely on the hippocampus, but carry out inherently opposing tasks – of matching and mismatching.

Handling interference is a crucial task of a memory that operates on similarities and dissimilarities, and on matches and mismatches. Because interference can happen both at encoding and at retrieval of records, our memory is adapted to handle it both at encoding and at retrieval. The hippocampus is implicated in resolving interference at both of these stages, but is often also supported by the prefrontal cortex. At encoding, for instance, the hippocampus can prevent interference without engaging the prefrontal cortex through so-called remapping. In remapping, distinct records can be produced for similar environments and in response to even minor changes in external (sensory) and self-generated (cognitive) inputs (Muller, Kubie, Bostock, Taube, & Quirk, 1991; Colgin, Moser, & Moser, 2008), acting as a mechanism of pattern separation, and prevention of future interference. But in other situations, it perhaps needs to cooperate with the prefrontal cortex.

In general, creating novel records, that is, encoding experiences that do not overlap with the previous ones, relies predominantly on the hippocampus (Preston & Eichenbaum, 2013). But when new experiences overlap with the existing records, both the hippocampus and the prefrontal cortex are critical to initial encoding of experiences. The prefrontal cortex is critically engaged in integration of new experiences into the retrieved records because when new experiences occur, they often, to a certain extent, conflict with the pre-existing model of the world. This conflict can be only resolved by the ultimate conflict resolver in our brain: the prefrontal cortex. The prefrontal cortex exerts top-down influence on a range of psychological processes, which is called the *executive control* (Shallice & Burgess, 1996; Smith & Jonides, 1999; Miller & Cohen, 2001). It serves as a centralized executive system from distributed models of memory, which in mammals actually comprises of a network of interconnected neocortical areas that send and receive projections from both sensory and motor systems (Miller & Cohen, 2001). This network involves various areas of the prefrontal cortex, such as medial, anterior, posterior and other, but for the sake of clarity, these specific areas will be reported in brackets to not confuse less neuroanatomically inclined readers. Overall, the prefrontal cortex is responsible for handling such tasks as strategy selection (Monsell, 2003; Block, Dhanji, Thompson-Tardiff, & Floresco, 2007), direction of attentional resources (Banich et al., 2000; Daffner et al., 2000; Asplund, Todd, Snyder, & Marois, 2010) and inhibiting prepotent behavioural responses (Aron, Robbins, & Poldrack, 2004; Chambers et al., 2006; Verbruggen and Logan, 2008; Jonkman, Mar, Dickinson, Robbins, & Everitt, 2009). Studies with rats revealed that prefrontal cortex (medial) is responsible for shifting attention between competing strategies, attentional targets, and behavioural response tendencies (Peters, David, Marcus, & Smith, 2013), which means that it is broadly involved in resolving competition (Badre & Wagner, 2007; Blumenfeld & Ranganath, 2007). Impairing the prefrontal cortex impairs an ability of accurate and rapid resolution of competing responses to changing circumstances, which is key for so-called *behavioural flexibility* (Block et al., 2007; Ragozzino, 2007). Because the prefrontal cortex is key for resolving competition between behavioural responses to current experiences, it was proposed to play a role also in resolving competition between records of past experiences. Indeed, the human prefrontal cortex was found to not only respond to the existence of competition between memory traces, but also to show an increasing activation with an increasing competition between the traces (Sohn, 2003).

Relevance

Equipped with this information, we can move on to exploring the complex relationship between the hippocampus and the prefrontal cortex. I have already mentioned that retrieval of stored traces is triggered by a cue that partially shares some patterns with the to-be-retrieved traces. When cues enter the sensory input, sensory areas in the brain process the information in the cue and transmit it to the hippocampus (Anderson, Bunce, & Barbas., 2016). In the hippocampus, the information in the cue triggers pattern completion and activates the traces recorded in the original past experience (Bartsch, Döring, Rohr, Jansen, & Deuschl, 2011; Eichenbaum, Yonelinas, & Ranganath, 2007; Rugg & Vilberg, 2013). What we have not learned yet, is that, afterwards, the hippocampus sends the information about the retrieved traces to the prefrontal cortex, as was showed both in rats and in humans (Preston & Eichenbaum, 2013). Upon pattern completion, a certain part of the hippocampus (anterior in humans, ventral in rats) retrieves a general context of similar past records, and the information about this general context is sent to the prefrontal cortex (medial). Once this information is processed in the prefrontal cortex, it is sent back to another part of the hippocampus (posterior in humans, dorsal in rats) which, finally, is responsible for retrieving a concrete record of an individual most relevant record.

The hippocampus can retrieve memories without the input of the prefrontal cortex, so why would it bother exporting any information to the prefrontal cortex? As we already know, we store a multitude of similar past experiences that overlap with each other and because of this overlap, are all potentially relevant for resolving the current situation. Since these experiences compete for retrieval and potentially lead to conflicting behavioural responses, a third-party conflict resolver must step in and decide which experience should ultimately guide our behaviour. This is what the prefrontal cortex does. But how does it support the selection of the most relevant trace? The prefrontal cortex has at least two mechanisms of doing just that: on the one hand, it accumulates and employs contextual information, and on the other, it spurs suppression of competing, but less relevant traces.

The prefrontal cortex needs to cooperate with the hippocampus to build and use the contextual information, and subsequently guide the retrieval. A context is a specific collection of patterns that is repeated across closely related experiences. When experiences occur within a single context, a certain part of the hippocampus (anterior in humans, ventral in rats) sends the context-defining information to the prefrontal cortex (medial). The prefrontal cortex gathers these pieces of information about different contexts and develops distinct records of these contexts. When an individual is put into a familiar context, the hippocampal signals with contextual information are again sent to the prefrontal cortex (medial), which then matches it with an appropriate context, and uses this context to resolve conflicts between individual traces stored in the other part of the hippocampus (posterior in humans, ventral in rats). The prefrontal cortex thereby engages context-appropriate traces, but can also suppress those traces that are context-inappropriate. Because signals sent to the hippocampus by the medial prefrontal cortex are also incorporated into hippocampal records, the prefrontal cortex (medial) prevents future interference between traces by training the hippocampus in retrieving patterns encoded in similar contexts (Guise & Shapiro, 2017).

The prefrontal cortex can decide what is relevant (context-appropriate) and irrelevant (context-inappropriate), and so guide the selective memory retrieval according to relevance. It can also suppress the competing yet irrelevant traces (Hasher, Zacks, & May, 1999; Hasher, Lustig, & Zacks, 2007; Anderson & Spellman, 1995; Bjork, 1989; Zanto & Gazzaley, 2009; Healey, Campbell, Hasher, & Ossher, 2010), but this suppression comes at a cost because the suppressed competitors become less available in the future, falling prey to a mechanism called *retrieval-induced forgetting* (Anderson, 1994). Several mechanisms behind such forgetting have been put forward, including the competitive interference account (e.g., Raaijmakers & Jakab, 2013), the inhibitory account (e.g., Anderson & Green, 2001) and the context account (e.g., Jonker, Seli, & MacLeod, 2013), but to understand differences between these three accounts, let us first consider a typical test of retrieval-induced forgetting.

In the typical test of retrieval-induced forgetting, individuals first encode category-exemplar pairs, such as “fruit – lemon”, “fruit – apple” and “insect-fly”. Afterwards, they are cued to retrieve some pairs from some categories, for instance by seeing an incomplete pair of “fruit – le___”. In this case, they practice retrieval of “fruit – lemon”, but neither of “fruit – apple” nor of “insect-fly” pair. After a delay the individuals participate in a test that measures their recall for the exemplars encoded at the beginning of the procedure, that is “lemon”, “apple” and “fly”. Not surprisingly, the subjects recall “lemon” more readily than “fly” and more readily than “apple”, simply because they have practiced it. But they also recall “fly” more readily than “apple”. This tendency has been termed *retrieval-induced forgetting*. In general terms, it arises when individuals practice retrieval of some information and so gain a better access to the practiced information upon future retrieval (Carpenter, 2012; Delaney, Verkoeijen, & Spirgel, 2010; Roediger & Butler, 2011). However, better access to the practiced pieces of information comes at the cost of impaired retrieval of other, related pieces of information (Anderson 2003; Storm & Levy, 2012). Again, a mechanism that has an adaptive value – of supporting swift retrieval of often-used traces, has a darker side, in which competing yet irrelevant traces become less and less available, even if they might be crucial at some point in the future.

Three explanations of retrieval-induced forgetting have been put forward. Two of them assume that “fruit_le” cues retrieval of two competing exemplars: “lemon” and “apple”. According to the first, the competitive interference account, selective retrieval of “fruit-lemon” increases the associative strength between “lemon” and “fruit” and then, when “fruit_le” cues retrieval of the associated exemplars, “lemon” interferes with “apple” and, as a stronger trace, blocks the retrieval of “apple”. Retrieving “lemon” does not have any direct impact on the strength of the competing “apple”, it is just relatively stronger than “apple” because of the practice. But according to the inhibitory account, strength of “apple” is directly weakened through suppression that facilitates resolution of competition between “lemon” and “apple” upon the retrieval cue. Successful retrieval of “lemon” requires inhibition of “apple”. Finally, the context account does not assume that “lemon” and “apple” compete for retrieval in its explanation of retrieval-induced forgetting. Instead, it suggests that the individual retrieves “fly” from the “insect-fly” pair more readily than “apple” simply because the category of “fruit” has appeared in both the encoding and the practice context, and the category of “insect” has appeared only in the encoding context. And whereas reinstating the encoding context benefits the retrieval of “fly”, and reinstating the practice context benefits the retrieval of “lemon”, neither of these contexts benefits the retrieval of “apple”. Therefore, relatively poorer retrieval of “apple” is a by-product of relatively better recall of “fly” after context reinstatement rather than an impairment of retrieving “apple”. Interestingly, recent findings revealed that both the context account and the inhibitory account may be correct. These two accounts come together in a two-factor account of selective memory retrieval (Bäuml & Samenieh, 2012; Dobler & Bäuml, 2012), in which selective memory retrieval triggers both the inhibition of competing memories and reinstatement of the retrieved items’ original encoding context.

Using “lemons”, “apples” and “flies” as experimental material could obviously only work with human subjects. To test whether retrieval-induced forgetting, just like other mechanisms described above, applies to animal memory, these cues need to take another form. Therefore, to adapt the above-mentioned procedure to sensorimotor skills of rats, Bekinschtein, Weisstaub, Gallo, Renner, and Anderson (2018) recently substituted the category-exemplar pairs from human studies with pairs of familiar and unfamiliar objects. The results confirmed that rats, like humans, have a control mechanism that, triggered by retrieval, initiates adaptive forgetting of competing traces. Taken together, these findings show that recalling and forgetting of past experiences is not determined solely by encoding, consolidation or reconsolidation. Some mammals (and perhaps some birds) dynamically interact with the stored records to support both current and upcoming behavioural goals, and can selectively retrieve what is usually relevant at the cost of gradual forgetting of what is usually irrelevant.

Survival is a matter of continuous selection. Selecting relevant over irrelevant pieces of information – both recorded in the past and available in the current situation – should be a basic task of animal and human memory. As Bekinschtein and colleagues (2018) have shown, rats could selectively retrieve goal-relevant memories: recognize familiar and non-familiar objects, and gradually forget those that were repeatedly irrelevant. But being susceptible to competition between overlapping memories is one thing, and overcoming such competition is another. If an animal could do the latter, it could change the way we think about animal memory.

Resolving memory competition arises when a cue triggers retrieval of at least two traces that, to a certain extent, overlap with the cue. Therefore, if we were to test whether an animal can resolve memory competition, we would need at least three situations: a current situation that would provide the cue, and two past situations, each of which would overlap with the current situation. Preferably, one of these past situations should be relevant for the resolution of the current situation, and the other should be irrelevant. I will return to this issue in the fourth part of this introduction.

In this part we have learned which mechanisms support a flexible memory system, and how their functions and malfunctions come about. Several of these mechanisms have been found both in humans and in animals; some, such as retrieval-induced forgetting, have been investigated predominantly in humans, and other, such as memory reconsolidation, have first been found in animals. All the mechanisms described in this section – of updating and resolving competition – allow for rapid and flexible adaptation to the ever-changing world; but their operation requires some tradeoffs. Memory reactivation allows for updating of the internal model of the world, but makes traces malleable. Resolution of memory competition allows for acting on relevant memories and not the irrelevant ones, but leads to gradual loss of the often-irrelevant memories, even though they might be relevant at some point in the future. Both of these mechanisms seem to be conserved across memory domains and mammalian species (reactivation: Agren, 2014; competition resolution: Bekinschtein et al., 2018).

In 1871 Charles Darwin suggested that the difference in memory (like other cognitive capacities) between “higher” animals and humans was *one of degree and not of kind* (Darwin, 1871). Two and a half centuries later one would think that we would have accepted this suggestion, since an impressive body of supporting evidence has been accumulated over the years. But this is not the case. Therefore, in the third part of this introduction, we should look at what has been thought and what is known about animal episodic memory, before moving on to outlining a shift in testing to what degree this memory differs from ours.

Part 3. What and how do animals remember?

In the beginning

The first definition of episodic memory was conceived in 1972, as we might remember from the first part of this introduction (Tulving, 1972). Its author, Endel Tulving, introduced it primarily to facilitate communication between researchers interested in human memory. Back then, as he wrote, "The distinction between episodic and semantic memory systems should not [have been] construed as representing the beginning of some new theory of memory" (p. 384). But, regardless of the author's intention, it has actually determined the direction of human memory research for the next 50 years. Interestingly, two decades after the initial publication, the theory of episodic memory was also extended to animal memory research, only to drive it – and indirectly taint it – for the years to come. To understand why this theory has been so influential, and how it led to everything that we know about episodic memory in animals, we need to have a closer look at how the theory has developed and changed after 1972.

That the book chapter from 1972 was a cornerstone of a new approach to memory research is perhaps not surprising. Even if it was not intended as a manifesto of the new approach, it was followed by a series of well-grounded publications in which Tulving and colleagues, on the one hand, continuously developed the notion of episodic memory, and, on the other, used it in ongoing debates about the nature and mechanisms of human memory. Up till 1979, Tulving and others focused on investigating how cues, traces and retrieval could be interrelated, often coming to conclusions that would be empirically proven in the years to come, and which we have – to a large extent – used in the two previous parts of this introduction. For instance, in 1974, Tulving discussed the term of the *cue* (Tulving, 1974); in 1975, with Watkins, he outlined a new theory of *memory trace* (Tulving & Watkins, 1975); and a year later, with Watkins and Ho, he discussed how retrieval depended on the context (Watkins et al. 1976). Furthermore, in a book chapter from 1979, Tulving argued that the retrieval depended on the compatibility between the cue and the trace (Tulving, 1979), which proved to be accurate as we have already learned in the preceding parts of this introduction.

The chapter from 1979 foreran two shifts: one in the theory itself, and another in the general approach to human memory research. How memory could operate was no longer the sole focus of the emerging theory; now the theory tackled two additional questions: how someone would use memory and how she would feel while using it. Because such use was necessarily preceded by retrieving the information from memory, what was happening at retrieval became more interesting than ever before. At that point in time, the notion of consciousness came into play for the first time, forerunning another shift – toward juxtaposing human memory with animal memory – that would come two decades later. The theory was further developed at the beginning of 1980s, thanks to case studies of amnesic patients (e.g., Schacter & Tulving, 1982a; 1982b; Schacter, Wang, Tulving, & Freedman, 1982), that is, patients that experienced difficulties in remembering past experiences induced by a certain event, such as a trauma to the head. These difficulties could be temporal or permanent and could either pertain to experiences from before the event in so-called *retrograde* amnesia, and/or, in *anterograde* amnesia, to those acquired after the event. In the first case, patients would not remember what happened with them in the past; in the second, they could not consciously retrieve memories acquired after the event that induced the memory loss.

Soon afterwards, and perhaps because of Tulving's interest in amnesia, consciousness started to play a prominent role in his theory; so much so that in 1985 episodic memory could no longer exist without so-called *autonoetic* consciousness. To understand how grave consequences this co-existence had for the future directions in memory research, and how it affected our understanding of animal memory, we first need to go back to the year of 1972, when the very first distinction between the episodic and the semantic memory system was outlined.

Episodic memory

The term of episodic memory is younger than that of semantic memory. *Semantic* memory was introduced earlier, in 1966, and was already quite established by 1972 (Quillian, 1966). It was defined as a memory structure (Rumelhart, Lindsay, & Norman, 1972), or a highly structured network (Collins & Quillian, 1969) that was responsible for remembering facts, concepts, words, images, and reasoning based on these items. In short, it allowed for understanding and using language.

However, as this term – of semantic memory – described only the linguistic part of memory domain, another term, that would refer to the non-linguistic parts of memory, was required. Otherwise, without naming these remaining parts, memory researchers could not communicate with each other as to what was common and what differed between linguistic and non-linguistic memory domains. Like short-term memory was juxtaposed with long-term memory, semantic memory also had to be juxtaposed with something. This juxtaposition was filled with Tulving's *episodic memory*, and therefore the distinction between the semantic and the episodic facilitated communication among memory researchers. These two memories – episodic and semantic – supposedly relied on two parallel systems that shared some common and some distinct characteristics (Tulving, 1972). Both systems selectively received information from perceptual systems and stored various aspects of the incoming perceptual information; both were also connected to other systems that translated this information into motor and cognitive responses, such as behaviour and conscious awareness. But each of the systems stored different kinds of information, retrieved and used it in different ways, and so was vulnerable to transformation and erasure of information to different extents. The original definition of episodic memory largely, but not fully, overlapped with what has been outlined in the previous parts of this introduction.

The episodic memory system was supposed to receive and retain information about temporally dated episodes and temporal-spatial relations between them. Simply put, it stored information on what, where and when happened in the past. This "what-where-when" information was not, however, filed as a separate experience that had nothing to do with the past ones; quite the contrary – each newly acquired record was stored in terms of autobiographical reference to the already existing contents of the episodic memory store. As a result, retrieving any record from the store had a twofold outcome: it made the record accessible on the one hand, and malleable on the other. For this reason, the contents of the episodic memory store were supposed to be prone to involuntary transformation and loss, to which they were particularly prone at retrieval. However, contrary to Kanerva's model, it was not the overlap in similar yet irrelevant patterns that was responsible for memory mistakes. In Tulving's theory, these mistakes originated from an overlap between temporal traces of the records.

The episodic memory system supposedly handled the experience of the world that heavily relied on perceptual information, but could also have been, to some extent, influenced by the information stored in the semantic memory system. The semantic memory system provided an organized knowledge about words and other verbal symbols, their meaning and relations, rules, formulas, concepts and any other language-based aspects of human knowledge. The semantic memory system did not register the perceptual information, but only its cognitive referent, that is a meta-level file of the information. Where the episodic system recorded a tiny, grayish and fluffy squeaking item with a long pink tail, the semantic system recorded the verbal category of the item: a rat. Because the semantic memory system was more detached from the perceptual input, this system, on one hand, allowed for the retrieval of information that was not directly stored in it, and on the other, was less prone to transformation and loss than the perceptually-driven episodic memory system.

To understand a fundamental difference between the episodic and the semantic memory system, we can consider the following example. Some of us drink coffee in the morning, and others do not. Asked, “Did you drink coffee this morning?”, we would perhaps give a positive or a negative answer. Regardless of the answer being “yes” or “no”, we could arrive at it in at least two different ways. We could have replied automatically, based on the knowledge of our morning habits; we usually drink coffee, therefore we drank some this morning, or we usually do not, therefore we did not drink coffee this morning. But we could have also remembered that, on that particular morning, we were sitting at the kitchen table, looking through the window and sipping coffee. If we did just that, we used our episodic memory system and gave an experience-driven answer. If, however, we gave a knowledge-driven answer based on our habits, then we used our semantic memory system.

This was the original meaning of these terms – of semantic and episodic memory. But a decade later, in 1983 and 1984, these meanings changed (Tulving, 1983; 1984). Now the two systems were not only accompanied by the third, procedural memory system, but the relationship between the original two was different as well. The three systems were fit into hierarchy with the procedural memory system at the bottom, the semantic memory system in the middle, and the episodic memory system at the top. The episodic memory system was no longer parallel to, but was considered a subsystem of the semantic memory system. The procedural memory system, which was introduced soon before by Cohen and Squire (1980), here was responsible for acquiring, storing and using perceptual, cognitive and motor skills. The semantic memory system dealt with knowledge that was represented symbolically, and the episodic memory system was responsible for personally experienced events (Tulving, 1985).

The three memory systems, however, were no longer discussed solely in relation to human memory. This time each definition was about “an organism” and its knowledge of the world. Because of the outlined hierarchy, the organism could not have the top, episodic memory system without having the middle, semantic memory system; and it could not have the semantic memory system without the bottom, procedural one. Setting the stage in this hierarchical way and referring to an organism when describing the procedural and the semantic system, but to a person when describing the episodic system, was not accidental. It was intentional and as such, it allowed for tying these memory systems to corresponding levels of consciousness. Soon afterwards it allowed for drawing a line between animal and human memory; a line that would ignite animal memory research in 1997, and fuel it for years.

Juxtaposition

Neal J. Cohen and Larry R. Squire were the first to introduce the term of procedural memory, based on their work with amnesic patients (1980). It seemed that some of these patients could acquire a mirror-reading skill as readily as healthy people, even though they had no conscious recollection of the learning sessions. The patients were conscious in the sense that they perceptually registered, operated on and responded to the situation, that is, they had access to so-called *anoetic* consciousness (Tulving, 1985). They acquired information and acted upon it without knowing that they did; this was what the procedural memory system allowed for. This system was placed at the bottom of Tulving's hierarchy in 1985.

We have already learned that we can give either knowledge-driven or experience-driven answers when asked about past situations, which we witnessed or participated in. The knowledge-driven answers are supported by the semantic memory system. We do not need to remember exactly what, how, where and when happened; we use our general knowledge to generate the answer. To give such answers, we need *noetic* consciousness. If we were limited to the immediately available environment, we could not tell whether we drank coffee this morning. Instead, we need to act upon our knowledge of "how things were/could be" that is detached from the current situation. Therefore, the semantic memory system requires noetic consciousness, the *knowing*.

On the contrary, giving the experience-based answer is only possible if we remember ourselves being present in the remembered past situation. We, and no one else, must have been the ones to sit at the kitchen table, look through the window and sip the coffee. To go back to that experience, we need *autonoetic* consciousness. Going back to the past is not available to amnesic patients that lost this kind of consciousness; they are stuck in a *permanent present* (Barbizet, 1970), and cannot become aware of own past and, likewise, of own future. Contrary to people with preserved autonoetic consciousness, they are incapable of *mental time travel* (Tulving, 1985). Without such consciousness, retrieving records of the past is further deprived of two characteristics. First, such retrieval lacks the special flavour or feeling that we acquired the retrieved experience; and second, it does not come with a sense of *subjective certainty* that allows us to estimate the likelihood of the experience actually belonging to us. Because both the flavour and the sense could be only reported verbally, it was assumed that the episodic memory system and autonoetic consciousness were available solely to humans. That the system was limited to humans was not explicitly uttered in 1985, but, while the procedural and the semantic memory systems were available to an *organism,* the episodic memory system was available to a *person*.

This version of the episodic memory system and its relation to other memory systems remained fairly similar for the next decade. In 1994, Tulving and Schacter, whose multiple studies were cited above, issued a book chapter, in which the authors themselves travelled to the distant past and to the near future. They outlined how views of memory changed over two centuries of memory-oriented thought and briefly discussed whether the distinction between various human memory systems could be mapped onto an analogical distinction between animal memory systems. The conclusions were rather sceptical. In principle, one could use such mapping to model and understand human memory in a better way, but one could not be sure how reliable the mapping would be. After all, "different species have evolved to solve problems of survival that are unique to them" (Schacter & Tulving, 1994; p. 30). Although many similarities in animal and human learning were established in behavioural and cognitive experiments prior to 1994, little was known about functional similarities of various brain areas in the human brain and the non-human brain. Direct comparisons were also hindered by the clear qualitative difference between the verbal reports and the non-verbal behavioural responses to experimental treatments, and by the mismatch between verbal instructions given to humans and the non-verbal ones directed to animal subjects. Simply put, too little was known about neurobiological differences between animals and humans, the animals could not speak, and we could not communicate with them in the same way as we could with humans. Therefore, outlining any similarities between human and animal memory, although theoretically stimulating, required caution and restraint at that point.

In the same year, in 1994, Tulving, along with Hans H. Markowitsch (1994), reiterated the same thought in response to a paper on rat memory published by Howard Eichenbaum, Tim Otto and Neal J. Cohen (1994). Because a method of getting animals to reflect on their past experiences, or measuring their conscious recollection was not around, there was still no reason to attribute the episodic memory system to animals. A lack of evidence was taken as evidence of a lack, and until an animal would speak up about its personal past or future, it would not have been granted the access to the episodic memory system. The response from 1994 signalled the second and final major shift in the theory of episodic memory: a shift from focusing solely on human memory systems to juxtaposing them with animal memory systems.

Tulving, however, was not the first to explicitly express this juxtaposition. He did support it in 1999, but only two years after it was voiced by Thomas Suddendorf and Michael C. Corballis in a paper on "Mental Time Travel and the Evolution of the Human Mind" (1997). In the paper, the authors compared the then-existing evidence from animal cognition studies with Tulving's definition of human episodic memory, and did not manage to confirm that any animal had access to the human episodic memory system. This outcome was perhaps not surprising, as the author of the theory would most likely arrive at this conclusion at any stage from the 1970s, through 1980s, to 1994 and his response to Eichenbaum and colleagues' paper (1994). There was no sufficient evidence that animals had autonoetic consciousness, that they could “use their imagination to reconstruct the order of past events” (Suddendorf & Corballis, 1997, p. 141) or imagine future events, or that they could recognize own memories as memories.

This was the short story of how the convenient distinction between the semantic and the episodic memory system led, a quarter of century later, to the profound distinction between the animal and the human memory. The distinction from 1972 certainly drove animal memory research. But indirectly – through, on the one hand, introducing the gap between the organism and the person, and on the other, tailoring the definition solely to the human memory system – also somewhat tainted this research. The term of episodic memory gave rise to another term, of “episodic-like” memory, devised for testing and discussing an equivalent cognitive capacity in animals. On the one hand, embedding such “likeness” to human memory already at the terminological level, suggested that animal and human memory had something in common. However, as the original term of episodic memory had a connotation of the emphasis on the gap between animals and humans, using its derivative in animal memory research effectively further emphasised the gap between human and animal memory. Keeping to the original term, and grounding its definition in purely behavioural criteria when referring to animal memory, would perhaps emphasise the assumed continuity between animals and humans instead. Such shift – from episodic-like (e.g., Babb & Crystal, 2006b; Roberts, 2006) to episodic memory (e.g., Crystal & Smith, 2014; Basile, 2015; Crystal, 2018) – happened recently in rat memory research.

Using the term of “episodic-like” memory, and relating the relevant studies directly to the semantic/episodic distinction, determined a direction of animal memory research for years to come. This direction imposed continuous referring to Tulving’s works, even when the experimental setups used in animal memory research were not in fact inspired by these works (e.g., Osvath & Osvath, 2008). It seems, however, that recently this tide turned, as new directions in animal memory research started to emerge (Osvath & Martin-Ordas, 2014; Osvath, 2015; Lewis, Berntsen, & Call, 2019).

Direct comparisons between animal and human memory studies are perhaps necessary because they allow for locating different animal species, including humans, on a continuum of memory-related capacities. However, as long as these comparisons are based on dichotomous criteria, they will tell little about the way, in which human and animal memory may work, and how humans and animals use various memory-related capacities. Answering such questions should not rely solely on human memory studies, but also on computer models which allow for simulating how episodic memory may work. In general, these models do not discriminate against animals or humans, and already serve similar purposes – of simulating the processes behind various cognitive capacities – in psychological research and some branches of animal cognition research. Such simulation is used in the following way: the results generated in empirical studies are fed into relevant computer models; the models simulate how such results could be obtained, and generate certain predictions that follow from the simulation. These predictions are later tested in further empirical studies. A similar cycle could allow for shedding the burden of semantic/episodic distinction and pushing episodic memory research in new directions.

Even if the direction outlined in 1998 invited years-long critique from Tulving and Suddendorf and may have hindered other influences, such as those from computer modelling, it led to many illuminating studies of animal memory. Before we move away from this direction and toward other sources of inspiration for experimental setups, we should find out what was found in the last two decades of animal memory studies. We will start with mental time travelling, and then proceed to metacognition and monitoring of subjective uncertainty.

Into the past

In 1985 and onwards, the episodic memory system has been considered key for mental time travelling, for instance, backward in subjective time to remember long-gone events from the personal past (Roberts, 2002). A smell, a taste, or a sound could kickstart this mental time machine, which would then land somewhere that we have already been so that we could relive something that has already happened.

Perhaps the most illustrious example of this ability was offered by Marcel Proust in his novel on "Remembrance of Things Past" (1919). One day, after coming home from work, the narrator's mother treated him to a cup of tea and a piece of a madeleine cake. Nothing was unusual about the shape of the cake or the dull and greyish afternoon, and nothing suggested that the day would get any better. However, as it soon turned out, the taste of the cake, soaked in a spoonful of tea, was enough to change it: detach the narrator from his surroundings and allow him for travelling back to his childhood years.

After the first bite, the depressing feeling of self-pity faded away, and a mixture of detachment, excitement and joy took its place. The familiar yet forgotten taste of the cake immediately pervaded the narrator's senses, but it took him a while to find the matching record. Once and only when the present was reconnected to the sought-after past, the narrator found himself in another place and another time. All of sudden he recognized the taste of another madeleine cake; the one that his aunt Leonie treated him to in her bedroom after dipping it in a cup of tea. He remembered that it took place "on Sunday mornings at Combray (because on those mornings [he] did not go out before church-time" (Proust, 1919, p. 70).

This story has been repeatedly used as generated by the episodic memory system (e.g., Yonelinas, 2007; Conway, 2008), although some did not share this view, as the childhood memory was, to some extent, involuntarily brought back by the taste and not sought after by the narrator (Neisser & Libby, 2005). However, the narrator's memory would be involuntary and not episodic, only if the taste of the cake immediately and directly brought back the recollection of aunt Leonie's room on Sunday mornings. This was not the case; because, upon the feeling of detachment, excitement and joy, the narrator actively sought after the relevant episode, this example did illustrate an episodic memory. In any case, we will use this example to understand the notion of mental time travelling into the past, and issues that arise upon closer inspection of the term.

The temporal dimension of the remembered event was an important aspect of Tulving's definition of the episodic memory system from the very beginning. Each past episode was supposedly time-tagged, and the overlaps between these time tags could lead to confusion upon retrieval. Such time-tag was present in the Proust's example: the original episode took place on one of the Sunday mornings. Not on a specific date, not in a specific month or even year, but a specific time of the day.

The dates of past situations are actually a very poor cue for the retrieval of the records stored in our memory (Barsalou, 1988; Brewer, 1988; Wagenaar, 1986). This happens because our records are not commonly time-dated. Such dating would make sense only if we thought about our past as a timeline on which the specific dates could be marked, but this is not the case (Friedman, 1993; 1996). Just like the narrator in Proust's novel, we usually cannot recall the dates, but we can rather precisely remember the time of the day on which something occurred (Friedman & Wilkins, 1985). There are at least two explanations of this fact. First, the time of the day is as much a matter of perception as objects or space; it can be extracted from the record of the past situation. Remembering the light, natural or artificial, dim or bright, perhaps reliably tells us something about the time of the day, but not the date.

Another explanation was put forward by Steen F. Larsen, Charles P. Thompson, and Tia Hansen: our memory of time may rely on cyclical temporal patterns such as day-night cycles, and therefore is actively reconstructed by applying general knowledge of such temporal patterns (Larsen et al., 1995). These patterns are relevant for our recurring every-day activities, and so, over time, we develop certain schematic general knowledge of these patterns. We perceptually pick up the regular occurrence of the every-day activities, which thereby become a part of the scheme by relation to the recurrent patterns of the natural environment (Friedman, 1993). For this reason, we are more inclined to relate the timing of the situation to these cycles rather than the clock or the calendar.

We are dependent on these cyclically recurring patterns, but our life is not a cycle; it is linear. And to make sense of our personal past, we need to somehow organize it in a more-or-less chronological, linear manner. For this purpose, we developed several ways of guessing an approximate date of the past situations. The dates of the past situations are usually reconstructed or inferred from the context in which the situation was recorded or from its relation to other components of our memory for the structure of time (Friedman 1993, 1996). Alongside the general knowledge of temporal patterns, we develop a personal temporal framework. This framework is based on some salient situations or periods in our life, to which we can later relate less salient situations that lack the time-date stamp. Within this framework, we can infer the approximate time of less salient situations in at least three ways: (1) we may remember how long ago the situation occurred from a certain time-dated situation (according to trace strength theories); or (2) we may remember when the event occurred on a certain time-scale (according to time-tag theories); or (3) we may remember the order in which certain situations occurred (according to event-succession theories; Friedman, 1993; Larsen et al. 1995). However, it must be noted that using both general knowledge about temporal patterns and the personal temporal framework for time-dating of events should be a domain of the semantic, and not the episodic system. It is the semantic system that is responsible for knowledge-driven cognitive references (Tulving, 1972), to which such temporal structures inevitably belong.

In 1997 Suddendorf and Corballis listed *temporal order* among the pre-conditions of the episodic memory system (1997). Although it was unclear which temporal-related capacity should be sought after in an animal – being sensitive to temporal order, using knowledge of temporal order, or another – this pre-condition has been taken seriously by animal memory researchers. Already a year later, Nicola S. Clayton and Anthony Dickinson addressed the notion of the *temporal order* in the first paper on episodic-like memory in an animal species, the Florida scrub jay. Just like ravens, jackdaws or magpies, scrub jays belong to the family of corvids and, just like the other family members, are food-hoarders. This means that scrub jays cache (hide) food in several locations when it is available and retrieve it later, when food availability drops (Pravosudov & Roth, 2013). Like other food-hoarding species (Hadj-Chikh, Steele, & Smallwood, 1996; Reichman, 1988; Gendron & Reichman, 1995), they adapt caching and recovery strategies to perishability of food items. They first retrieve the items that are the most perishable (Clayton, Mellor, & Jackson, 1996), that is, have the shortest expiry date. To retrieve no longer visible food items after a delay, scrub jays perhaps need well-developed memory for what, where and when they cached. Remembering the location is crucial for the scrub jay's survival; remembering what was cached allows for extracting the more preferred item before the less preferred; and remembering when the item was cached allows for extracting the perishable items before the non-perishable ones. Therefore, food-caching behaviour makes the scrub jay a good candidate for so-called *episodic-like* memory studies, known also as *what-where-when* studies.

This term – of episodic-like memory – was introduced by Clayton and Dickinson (1998) as an animal counterpart of Tulving's episodic memory, and resulted from an attempt of coming up with purely behavioural criteria of such memory in animals. Because autonoetic consciousness could not be shown with an absolute certainty in a non-verbal creature, this criterion was excluded from the definition of episodic-like memory. Instead, the episodic-like memory was operationalized as an integrated memory for “what”, “where” and “when” happened in the animal’s past, and was first tested in a cache-recovery setup. This operationalization followed Tulving’s definition from 1972, which did not assume that autonoetic consciousness was prerequisite for episodic memory.

In the cache-recovery setup, up to three delays and up to three types of food items are introduced. The delay scheme usually includes a short and a long one (e.g., Clayton & Dickinson, 1998), or a short, a medium and a long one. The food items differ in perishability, that is, the time it takes for them to become inedible. Peanuts are typically used as the least perishable food item, crickets as the item that degrades sooner than the peanuts, and wax worms as the item that degrades the soonest. The delays are then paired with the food items. Without any intervention on the experimenter’s part, after the short delay, all of these items would be edible. After the medium delay, wax worms would be no longer edible, and after the long delay, both wax worms and crickets would become inedible. As fresh wax worms and crickets are preferred over fresh peanuts, the birds should have chosen wax worms and the crickets over peanuts, whenever all of these items were still edible.

At the beginning of an experiment with the cache-recovery setup, naïve birds do not know about these relationships. Some of them acquire this knowledge in a training phase, and others do not. Those that learn the relationship are tested in a so-called “Degrade” group. Those that do not, belong either to a “Replenish” group, in which all food types are present and edible at all times, or to a “Pilfer” group, in which the perishable items were no longer present in the caches after the long delay

Clayton and colleagues carried out a series of studies with this setup (1998, 1999a, 1999b, 2001, 2003, 2005). In the original study from 1998 the scrub jays, that learned the relationship between availability and time delay adapted their cache recovery behaviour to maximize the gain from the task. They were more likely to go for the more preferred, but quickly degrading wax worms after a short delay, and more likely to go for the less preferred, but non-perishable peanuts after a long delay. Two further studies published in 1999 confirmed this tendency (1999a, 1999b), but regardless of the findings, it was still not clear whether episodic-like memory was behind the scrub jays’ behaviour. The birds could have used other strategies to judge whether the hidden food items were still available after the delays. For instance, the scrub jays could have kept track of the time that lapsed since caching, and use it as a discriminative stimulus for the choice between the peanut and the worm caches (Roberts, 2002). Simply put, they could have used a simple algorithm: if little time passed, go for the worms; otherwise go for the peanuts. Alternatively, the birds could have gone for worms if no night has occurred in between the caching and the recovery, as the short delay equaled only 4 hours. If the night occurred (and in fact five did during the long 124-hour delay), they could go for the peanuts.

The studies from 1998 and 1999 could, in principle, measure the use of search-avoid rules rather than the use of the episodic-like memory system (Clayton, Yu, &

Dickinson, 2001). To distinguish between these two explanations, in 2001 Clayton and colleagues employed a slightly different experimental design (2001). This time, the scrub jays first learned the relationship between three delays and the perishability of two food items; some learned on peanuts and wax worms, and others on peanuts and crickets. After 4 hours, always both items were edible. But after 28 hours the birds in the wax-worm group could only go for the peanuts, as the worms were already inedible. On the contrary, after the same delay of 28 hours, the birds in the cricket group could still go both for the crickets and for the peanuts, as both items were in a fine condition. Finally, after 100 hours, in both groups only peanuts were a good choice, as all other items had already degraded.

In the next step, the scrub jays from both groups were confronted with wax worms and crickets. Each bird already knew how perishable was one of these items in relation to the peanuts, but nothing about the other item. Therefore, the bird had to use its knowledge of relative perishability in a new context and act accordingly. Repeating a previously learned response associated with the length of delay or the presence of night in between caching and recovering was no longer available simply because the bird had no previous experience with one of two items. The characteristic of the unfamiliar item had to be inferred from another, somewhat overlapping experience. The memory of the past situation now had to be used in a flexible manner.

However, this finding again found another explanation. Soon afterwards, in 2002, William A. Roberts suggested that the birds perhaps used "some correlate of elapsed time to discriminate recent from more distant bouts of food caching" (Roberts, 2002, p. 486). The birds could have used the already-mentioned human strategy of comparing the relative strength of records; if a trace of worm caches was weaker, it meant that the worms had likely degraded; and if it was stronger, it meant that the worms were likely still edible. Only later, around 2010, cues of such strength were controlled in studies with rats (Zhou & Crystal 2009) and black-capped chickadees (Feeney, Roberts, & Sherry, 2011b), and revealed that they remembered at which point in time something had happened, even when relying on how-long-ago information was no longer possible.

Showing that the scrub jays could use previous knowledge to solve an unpredictable situation, in which they had to infer how long an unfamiliar food item would last, provided the first clear evidence of memory flexibility. It was published right after Tulving's assessment of the episodic-like memory studies, in which he suggested that they came close to showing that the scrub jays' memory was indeed episodic (2001). Clayton and colleagues were called out to demonstrate whether the birds could act flexibly based on "what"-"where"-"when" memory, as such demonstration "would constitute another step in the emancipation of birds, or other animals, as episodic creatures" (Tulving, 2001, p. 1513). Regardless of Clayton and colleagues' findings, adding the requirement of flexibility to the definition of episodic memory was somewhat unexpected. In the original definition from 1972, the episodic memory system did not include any cognitive tools of inferential reasoning or generalization. It was the semantic memory system that operated on the records of the episodic memory system, and from these records could generate something that we did not actually learn (Tulving, 1972).

This sudden requirement of flexibility perhaps came from the above-mentioned paper by Suddendorf and Corballis (1997). The authors wrote, "mental time travel by humans (…) allows a more rapid and flexible adaptation to complex, changing environments" (Suddendorf and Corballis, 1997, p. 133) and further, that "the ability to mentally travel in time is (…) in itself characterized by generativity and combinatorial flexibility" (p. 133). Although that memory flexibility would drive the rapid and flexible adaptation to complex environments was not Tulving's idea, and its relation to the pillars of the episodic memory system was not clear, we should agree that it is perhaps an important aspect of human and animal memory.

Apparently, the scrub jays could act flexibly in never-experienced situations. And even if they did rely on the record strength in 2001, in 2003 and 2005 they no longer could. In 2003, Clayton and colleagues showed that the scrub jays could update memory with new information that was not available at encoding, but only in the delay between encoding and retrieval. In 2005, the scrub jays flexibly adapted own caching strategies to the conditions at recovery. And soon, from 2007 onwards, Clayton and colleagues' interests shifted to animal foresight and planning, that is, mental time travelling into the future.

Into the future

At the beginning of the previous section, only one direction of mental time travelling was mentioned – backward, that is, into the past. But, in the earlier parts, we learned that memory allows for generating predictions about potentially upcoming situations. Therefore, it allows not only for projecting oneself into the past and remembering (re-experiencing) the past situations, but also for projecting oneself into the future and imagining (pre-experiencing) the possible ones (Raby et al., 2009). As Tulving wrote in 1985, without this ability, an amnesic patient called N.N. was stuck in a "permanent present" (1985, p. 4). This notion – of being stuck in time – was later used by Suddendorf and Corballis (1997), and Roberts (2002) – to suggest that animals, likewise, lived in the permanent present, as they could go neither backward nor forward in their subjective time. We have already learned that several experiments were devised in the years to follow, and showed that animals could use what-where-when memories of the past to guide own behaviour in the present, even if the overlap between the past and the present situation was only partial (Clayton et al., 2001). In fact, since 1998, the what-where-when paradigm has been translated into a range of experimental setups and tested with a range of animal subjects, such as rats (e.g., Eacott & Norman, 2004; Babb & Crystal, 2005, 2006a, 2006b, Kart-Teke, De Souza Silva, Juston, & Dere, 2006), mice (Dere, Houston, & De Souza Silva, 2005), meadow voles (Ferkin et al. 2007), pigeons (Zentall et al., 2001; Skov-Rackette et al., 2006), black-capped chickadees (Feeney, Combs, delBarco-Trillo, Pierce, & Franklin, 2009), magpies (Zinkivskay, Nazir, & Smulders, 2009), orangutans, chimpanzees and bonobos (Martin-Ordas, Haun, Colmenares, & Call, 2010; Martin-Ordas, Berntsen, & Call, 2013), gorillas (Schwartz, Colon, Sanchez, Rodriguez, & Evans, 2002; Schwartz, Hoffman, & Evans, 2005), and even cuttlefish (Jozet-Alves, Bertin, & Clayton, 2013) and zebrafish (Hamilton et al., 2016). Regardless of all these findings, some remained unconvinced as to whether animals could travel into personal past and vehemently undermined these findings (Suddendorf & Corballis, 2010), until further evidence of animal capacity for planning emerged from prospective cognition studies (Corballis 2013; 2014). Engaging in prospection, that is, in thinking about possible future events, has received various names – of future planning (Clayton, Bussey, & Dickinson, 2003), and episodic future thinking (Atance & O'Neill, 2001; Russell, Alexis, & Clayton, 2010), but they both refer to an ability of projecting oneself into a potential future situation.

Prospective cognition studies involve testing whether an animal could detach itself from its current motivation and act ahead of future needs (Raby, Alexis, Dickinson, & Clayton, 2007). That an animal is not capable of such detachment, was a hypothesis put forward by Bischof (1978) and Bischof-Köhler (1985), known as the *Bischof-Köhler hypothesis.* According to this hypothesis, all behaviours that are performed by animals in the present situation, but would lead to a certain outcome in the future, must have been driven by a current need that could be removed by this outcome (Roberts & Feeney, 2009). To test whether this statement was true, various experimental setups were devised in the recent years, each of which falls more or less into one of the following groups: (1) in the first group of studies, animals could select one of alternatives that led to different outcomes in the future (squirrel monkeys: McKenzie, Cherman, Bird, Naqshbandi, & Roberts, 2004, Naqshbandi & Roberts, 2006; black-capped chickadees: Feeney, Roberts, & Sherry, 2011a); (2) in the second group, animals could save food for the future by moving it from one location to another (Correia, Dickinson, & Clayton, 2007, Raby et al., 2007, Cheke & Clayton, 2012); and (3) in the third, animals could save a tool for the future, likewise by moving it from one location to another (Mulcahy & Call, 2006a; Osvath & Osvath, 2008; Kabadayi & Osvath, 2017). To understand what the actual setups looked like, let us consider one setup from each group, starting from Naqshbandi and Roberts's, through Raby and colleagues', to Osvath and Osvath's.

Mariam Nashqbandi and William A. Roberts offered two choices to the tested squirrel monkeys: the animals could either choose four dates or one date (2006). Eating dates made the monkeys thirsty. They normally preferred four dates over one, and when they soon got thirsty after eating the fourth, they could quench the thirst thanks to an unlimited access to water. In the experiment, they were given the same choice, but this time the water bottle was not accessible for a certain period after the choice; it would be returned either 30 minutes later, if the monkey chose one date, or 3 hours later, if the monkey chose four dates. Upon the choice, the monkey was not thirsty and so, according to the Bischof-Köhler hypothesis, it should not be able to anticipate the future thirst and act ahead of it. The monkey should, therefore, choose four dates over one, in accordance with its current lack of thirst. However, this was not the case – the monkeys reversed their preference and, as long as the water access was limited, they were more likely to choose one date over four.

Further evidence against the Bischof-Köhler hypothesis was provided by Caroline R. Raby and colleagues (2007) thanks to a so-called “planning for breakfast” experiment with western scrub jays. Normally, the birds had an unlimited access to food during the day, but at 17:00 they were separated from their partner and introduced to a three-compartment setup, in which the bird could access the two side compartments (A and C) from the middle one (B). Overall, the bird spent 2 hours there, but from 18:30 onwards it could access a bowl with pine nuts; the nuts were powdered to prevent the bird from caching. At 19:00 the bird returned to its partner and did not receive any food overnight. On the next day, at 7:00, it was again introduced to the experimental space for two hours, and was either confined to compartment A, or compartment C. In one of these compartments, for instance A, the bird would again receive powdered pine nuts; but in the other, for instance C, it would not receive any food. After six days, on which the bird spent the two morning hours thrice in compartment A, and thrice in compartment C, it was ready for the test. Then, in the evening, instead of receiving powdered pine nuts, it received whole ones, which it could both eat and cache in the trays available in compartments A and C. The scrub jays were more likely to cache the whole nuts in compartment C, as if anticipating the risk of hunger on the following morning. Although seemingly this experiment allowed refutation of the Bischof-Köhler hypothesis, it was not clear whether the birds indeed anticipated the hunger or just cached the food in a place that they associated with previous hunger (like rats, Roitman, van Dijk, Thiele, & Bernstein, 2001). Therefore, a follow-up experiment introduced another food item – kibble – alongside the pine nuts, and this time each food item was served in one of the compartments during breakfast, for instance the kibble in A, the pine nuts in C. In an analogical procedure to this described above, when given an opportunity to cache whole, and not powdered, food items in the evening, the scrub jays were more likely to cache the kibble in compartment C, and the pine nuts in A, perhaps to ensure the access to both food types in any compartment on the following morning.

The final experimental setup was used by Mathias Osvath and Helena Osvath (2008) to test whether an orangutan and two chimpanzees could choose and safe-keep a tool that was useless in the current context, but would allow for retrieving a reward in the future. This setup, to some extent, would fall into the first group of studies that tackled the Bischof-Köhler hypothesis because in one of the procedures it actually offered the animal two choices: either a small reward in the present, or a tool that warrants a larger reward in the future. First, the ape learned to use the tool – insert a plastic hose into an apparatus and suck a fruit soup out of it; all apes mastered it in a single trial, after observing the experimenter's demonstration. In the next phase, while being able to look at but not access the apparatus, the apes were allowed to select one object out of four, among which was the functional hose. This selection procedure was then repeated in the experimental trials without any, including visual, access to the apparatus at the selection. After making the selection, the ape left the "selection" room with the tool, went back to its social group, and, once 70 minutes passed, was allowed to a separate "reward" room in which the apparatus with the fruit soup was available. This procedure was repeated in total in four different conditions, but we will focus on the one, in which the apes had to choose between an immediate yet smaller and a delayed yet larger reward. Now, alongside the hose and random nonfunctional objects, a piece of favourite fruit was available for selection, but as only one object could have been selected, grabbing the food item would remove the ape's chance for the access to the fruit soup in the future. Overall, the apes were more likely to select the hose and risk its loss in the social group, but nevertheless wait for the larger reward that would be accessible only after 70 minutes than the piece of favourite fruit. Later, the apes were also able to select a novel different-looking functional item, such as a white plastic pipe, a hollow aluminium frame, and a hollow bamboo stick, over novel nonfunctional items such as discarded wrist watch, green pencil or blue nylon rope (Osvath & Osvath 2008, p. 670). Therefore, the apes, similarly to the scrub jays, displayed a flexible behaviour which was not constrained only to those situations that fully overlapped with the records of the past.

Osvath and Osvath's (2008) setup was somewhat similar to a so-called Spoon Test, which was earlier put forward by Endel Tulving as a way of testing one's prospective cognition (Tulving, 2005; Scarf, Smith, & Stuart, 2014). This test was inspired by an Estonian story, in which a young girl has a certain dream. At her friend's birthday party, the girl is treated to her favourite chocolate pudding, which she, to her despair, cannot eat: as everyone but her brought their own spoon to the party, she was the only one who could not scoop up the pudding. To avoid the disappointment when she falls asleep the next day, she goes to bed with a spoon in her hand and with the chocolate pudding in mind. Doing so was supposedly a sign of autonoetic episodic memory. If any animal was able to pass this test, even the so-called *Morgan's Canon* could not restrict granting such species the access to this capacity. As an aside, Morgan's Canon is a principle in comparative psychology research, according to which each behaviour should be always interpreted as a sign of as simple and unadvanced cognitive capacities as possible, before referring to more complex and advanced ones (1894). We have already discussed an example of the Canon in action: the scrub jays' performance in one of Clayton and colleagues’ studies could have been interpreted either in terms of record strength (the simpler capacity) or episodic remembering of a past event (the more complex capacity). In that case, in accordance with the Canon, the record strength interpretation was chosen as the more plausible one (Roberts, 2002). Tulving’s Spoon Test was obviously passed by the orangutan and the chimpanzees in 2008, and later, in another task, again by chimpanzees (Osvath & Persson, 2013), orangutans and bonobos (Bourjade, Call, Pele, Maumy, & Dufour, 2014), and, recently, also by ravens (Kabadayi & Osvath, 2017).

The problem is that both passing the Spoon Test and all the other tests that have been briefly sketched out, did not convince some of the fiercest critics that the tested animals had access to mental time travelling. Quite frankly, it seems that nothing could be done within the mental-time-travelling framework that could put a stop to the influx of other possible explanations (e.g., Suddendorf & Corballis, 2007, Hoerl & McCormack, 2018), in which the results will be essentially boiled down to a range of associative learning schemes. However, it seems that, in the recent years, the debate around mental travel into the past and into the future shifted toward new experimental setups that test animal memory in its own right, allowing the debate to evolve in a new direction. As long as the juxtaposition between the animal and the human episodic memory lied at the core of comparative memory studies, this shift was not possible.

When in 1998 Clayton and colleagues turned Tulving’s idea of memory for “what”-“where”-“when” into an experimental setup, and adjusted it to scrub jays’ sensorimotor skills, they straightforwardly engaged in a debate which, from the very beginning, was aimed at showing the discontinuity between the animal and the human mind. This step has been repeated a decade later by Osvath and Osvath (2008) when they, unintentionally (M. Osvath, personal communication, 25 June 2019), used a method resembling the Spoon Test adapted to the apes’ sensorimotor skills. The debate perhaps came to a dead end when both directions of travelling in the subjective time have been, to a large extent, explored and yet this exploration did not bring about any consensus. Regardless of the above-mentioned results and others not reported here, we might never know whether an animal can project itself into the past and/or into the future, and travel backward and/or forward in its subjective time.

The definition of episodic memory that lies at the core of the years-long debate was devised specifically for humans, and therefore left little, if any, space for evolutionary continuity (Cheke & Clayton, 2010; Eacott & Easton, 2012). It was only one option out of many, as was hinted in the previous parts, but it just gained more attention than others. It might have been more accurate than others were, or it might have just been more controversial; maybe it was especially well grounded in the empirical evidence, or maybe it offered definitions that were built on dichotomies and sold better than the less clear-cut ones. There is no simple answer to these questions, but it is perhaps an important issue that was for some years lost in the mental-time-travel debate: Tulving's theory was, and still is, just a theory. And while it offered a lot of insight into how human and animal memory could work, even its author changed it several times so that it could not be falsified by the incoming results.

Centering the debate around Tulving's and Suddendorf's view on the gap between animal and human memory did not allow for drawing on other, perhaps more useful sources of inspiration, such as computer models. This debate has been fuelled by a competition between the authors of the relevant animal memory studies, and the critics of these studies. Outside of such a competitive environment, many of the studies might have never been conceived. Heated debates, like any events that lead to emotional arousal, may enhance our processing of salient issues (e.g., Lee, Sakaki, Cheng, Velasco, & Mather, 2014) that are in the focus of the debate. In this case, the dichotomy between semantic and episodic memory, and between animals and humans, may have acted as such issues, and therefore gained special attention. However, such heated debates may also lead to an impaired processing of less salient issues (Lee et al., 2014), such as other, non-dichotomous findings from psychology. Therefore, it is perhaps not surprising that, until recently (e.g., Bekinschtein et al., 2018; Lewis et al., 2019), other inspirations from psychological studies took much less space, if any, in the debate. Reorienting the focus to novel influences, from psychology and/or computer modelling, would allow for further development of the field through, for instance, generating new empirical data, which could be fed into computer models in the future. Modelling of animal cognitive capacities (e.g., Kleyko et al., 2015), paired with modelling of equivalent cognitive capacities in humans, could shed more light on both the evolutionary continuity between different animal species and species-specific differences that underpin the observed differences in performance.

Many of the assumptions, that drove the debate for some years, were, in fact, unsubstantiated, as Osvath and Martin-Ordas (2014) pointed out in the recent years. For instance, Tulving (e.g., 2005) and Suddendorf (e.g., with Corballis, 2007) repeatedly suggested that autonoetic consciousness is prerequisite for episodic recall and episodic foresight, and that as long as the access to such consciousness is not established in an animal species, this species cannot be granted access to the episodic system. However, even in people, the causal link between the capacity for autonoetic consciousness and the episodic system is not grounded in empirical evidence (Osvath & Martin-Ordas, 2014). Although people report subjective experiences that are indicative of autonoetic consciousness, while using the episodic system, it remains unclear whether autonoetic consciousness is in fact prerequisite for episodic recall and episodic foresight, or is only an epiphenomenon generated when one uses the episodic system. Osvath and Martin-Ordas (2014) called for using behavioural and neurobiological indicators of the running episodic system instead. Turning to such evidence revealed that the core properties of brain areas and associations, which support the human episodic system, are in fact shared by all birds and mammals (Allen & Fortin, 2013). Therefore, in principle, the episodic system could potentially have evolved in all these animals, and, based on this finding, there is no reason for treating the episodic system as "more recently evolved" (Tulving, 2005, p. 11) than the semantic system. The assumption that these systems may have coevolved for years of evolutionary history (Osvath & Martin-Ordas, 2014) seems much more accurate, given the above-mentioned bidirectional relation between these systems in human memory. This relation was recently strengthened by a meta-analysis that showed a considerable neural overlap between the two systems (Binder, Desai, Graves, & Conant, 2009; Osvath & Martin-Ordas, 2014). Taken together, all these arguments reveal several problems of the dichotomies that governed the mental time travel debate on the one hand, and support the shift toward new, perhaps more fruitful, directions on the other.

Travelling – through time?

Do we really travel through personal time when re-experiencing the past or pre-experiencing the future? Or, in other words, do we use our minds as if they were time machines? In a fine-working time machine, we should be able to choose a certain year in the past, or in the future to determine our destination (e.g., Wells, 1895). Then the machine would take us back or forward to the problems of that particular situation so that we could tinker with them and change the course of history. The "why" and the "how" of our time-travel would then be completely different than those suggested by the outlined theory of mental time travelling. We would travel in time to deal with the problems of the past or of the future, and we would choose a specific time in which dealing with those problems was still possible. On the contrary, we use mental time travelling to deal with the problems of the present, and we are far too poor at coming up with the calendar referents of the situations (Friedman, 1993; 1996) to consider our mind a reliable time machine. And we do not store the records of the past on a chronological timeline (Friedman, 2007); we likely store them in a far more sophisticated way, for instance, split into traces and distributed over numerous locations (Kanerva, 1988). Perhaps our mental time travelling is not really about time, and neither is the animals'.

As mentioned above, the "when" aspect of episodic-like memory was the most controversial of the three because it could have related to different temporal aspects, such as "how long ago", "at which point in time", or none, such as "in which context". As we might remember, in 2002 Roberts suggested that if the scrub jays tested by Clayton and colleagues (Roberts 2002, Clayton et al. 2001) used the "how long ago" information, they did not necessarily engage their episodic-like memory; and only if they remembered "at which point in time" something happened, they would have used such memory. However, it seems that episodic memory does not necessary involve remembering any temporal aspects of the past situation. Ten years later, in 2012, Easton and colleagues found that in humans the recall of “what-where-how long ago” was associated with feeling of knowing rather than remembering, and conversely, the recall of “what-where-in which context” was associated with the feeling of remembering rather than knowing (Easton, Webster, & Eacott, 2012). Therefore, while recalling “in which context” engaged the use of episodic memory, recalling “how long ago” engaged the use of semantic memory. The record of the past situation can comprise of various traces, but these traces may as well contain no temporal information (Eacott & Easton, 2012). Therefore, it seems unlikely that our re-experiencing of the past situations and pre-experiencing of the future ones could be described as mental time travelling.

We do not use this ability to go back or forward to tinker with the long-gone or the much-delayed problems; we use the past problems and imagine the forthcoming ones to act in the present: to resolve the situations at hand. Although our records are for the use in the future at the moment of encoding (e.g., Klein, 2013; Osvath & Martin-Ordas 2014; Osvath, 2016), we can actually act upon these records only in the present. In other words, it is the present that links the past and the future, and gives us an opportunity to benefit from our episodic memory and future episodic thinking. If these two abilities rely on shared cognitive resources and/or common cognitive mechanisms, they must have more in common than autonoetic consciousness (Eacott & Easton, 2012).

The empirical link between episodic memory and future episodic thinking needs to be more robust, for instance, showing some neurophysiological underpinnings, accessible through recordings of brain activity (Corballis, 2013). This link has been recently identified as the already-mentioned *core brain network*, which supports not only episodic memory (Schacter et al. 2007; Buckner et al., 2008; Spreng et al., 2009), but also future episodic thinking (Buckner & Carroll, 2007). This network overlaps to a large extent with *default mode network* which has so far been identified in humans (Mason et al. 2007), chimpanzees (Rilling et al., 2007), rhesus macaques (Arsenault, Caspari, Vandenberghe, & Vanduffel, 2018; Vincent et al. 2007), mice (Stafford et al., 2014) and rats (Lu et al., 2012), and is considered responsible for various self-referential functions that have been traditionally considered to be uniquely human (Lu et al., 2012). Default mode network supports not only remembering and imagining (Buckner et al., 2008), but also sustenance of conscious awareness (Horovitz et al., 2009) and so-called *mind wandering* (Kajimura, Kochiyama, Nakai, Abe, & Nomura, 2016). We already know what remembering, imagining, and awareness mean, but mind wandering has not been defined yet. We engage in mind wandering on daily basis, when we do not need to attend to immediate goals and get lost in our own thoughts (Lu et al., 2012; Kam & Handy, 2014), for instance, recalling a conversation with a friend or wondering what we will wear to another friend’s party. The extensive structural and functional overlap in the default mode networks of the mentioned brains – of humans, chimpanzees, monkeys, rats and mice - could support the evolutionary continuity in the underpinnings of human and animal cognitive capacities. Furthermore, the default mode network perhaps serves the same function as Kanerva's memory system (1988), namely, it "evaluates internal and external body states by assessing information from multiple sensory modalities and, by integrating with past experience, anticipates changing environmental contingencies" (Lu et al., 2012; p. 3983).

Back to flexibility

When we think about the future, we can sample and recombine traces of the available records of the past (Szpunar, Chan, & McDermott, 2009; Szpunar & McDermott, 2008). For instance, when we imagine ourselves on a beach, the imagined beach would look like the beaches that we have actually seen before. And when we imagine a future event that could take place in a recently visited art gallery, it would perhaps be much richer in detail than an imagined event in a long-ago visited one (e.g., Arnold, McDermott, & Szpunar, 2011). However, such future scenarios cannot be based solely on recombined traces because, after all, we are able to imagine a scene that would take place in a jungle, even if we have not been to one before (Szpunar & McDermott, 2008). This shows that constructing a potential scene does not rely solely on our personal experiences; it can as well contain the input from semantic memory (Hassabis & Maguire, 2007; Schacter & Addis, 2007). Just like the record of the past has to be reconstructed from the traces that it was initially split into, the projection of the future has to be constructed from the available information.

Therefore, both episodic memory and episodic future thinking involve recombining the retrieved information, and both are influenced by the input from semantic memory. The capacity for such recombination is a cornerstone of memory flexibility. If we can select currently relevant components of the past situations over the irrelevant ones, we can deal with and prepare for dealing with situations that do not fully overlap with these past situations. Two abilities that support such selection were identified in the recent years. The first one, called *combinatorial flexibility* (1997, p. 134) or *recursion* (2007, p. 307), was introduced by Suddendorf and Corballis. Recursion allows for generating many possible situations out of a finite set of familiar traces, just like many melodies can be generated out of a finite set of tones. The second one, called *self-control*, allows for suppressing immediate behavioural tendencies in favour of delayed rewards, and according to the Bischof-Köhler hypothesis, was available only to humans. In 1997, Suddendorf and Corballis suggested that the "animals' [had a] general problem with simultaneously representing conflicting mental states" (p. 145), and that "the flexibility of the newer system allowed [humans] to consider different options, whereas inherited instincts or insight-free acquisition of response patterns were effectively fixed by the motivational state of the organism and by environmental contingencies" (p. 147). Therefore, what actually made animals different from humans was this ability to simultaneously consider conflicting options, select one over another and act upon it regardless of the current affective state and the misleading aspects of the current environment.

Although Clayton and colleagues (2001), Correia and colleagues (2007), Naqshbandi and Roberts (2006), and Osvath and Osvath (2008) all tested whether animals could use previously acquired information in a novel context (Salwiczek et al., 2010), it seems that these teams tested two different underlying abilities. On the one hand, Clayton and colleagues (2001) tested whether the scrub jays had access to recursion and could recombine a certain set of information acquired in the past to guide behaviour in the present. On the other hand, Correia and colleagues (2007), Naqshbandi and Roberts (2006), and Osvath and Osvath (2008) tested whether the scrub jays, the squirrel monkeys, and the great apes had access to self-control and could use a certain set of currently available information to guide both present and future behaviours. In other words, Clayton and colleagues' study (2001) did not induce any conflicts between mental states but involved information acquired in the past. On the contrary, self-control studies did induce a conflict between concurrent mental states but involved currently available information. Therefore, self-control, but not recursion, studies induced the conflict between simultaneously represented mental states that would potentially lead to two different responses to the situation at hand. However, this conflict was between the present and the potential future. It was not about several situations in the past that were partially conflicting with the present. That is, the memories of the animals were not in conflict in the self-control or recursion studies – there was either a possible future which conflicted with the present, or several non-conflicting memories that could be combined. Therefore, neither recursion nor self-control studies tested whether the animals could resolve conflicts between two records that partially overlapped with the current situation but spurred contradictory behavioural responses. This ability – of resolving conflicts between partially overlapping records – could drive a different kind of flexibility than recursion and self-control, which has been overlooked in animal memory research. In this thesis, I suggest that the ability of resolving conflicts between partially overlapping records could considerably boost one's behavioural flexibility. First, this ability would allow for choosing the most relevant option from among different conflicting ones, generated from the records of the past. Second, this ability would allow for choosing the most profitable of two conflicting options that stem from the past, and not only from the present and the future.

Several studies showed that animals were able to apply previously gained knowledge about perishability and functionality of certain items to a novel, partially overlapping situations (e.g., Clayton et al., 2001; Osvath & Osvath, 2008).

However, none tested whether animals could resolve an internal conflict between records that partially overlapped with the current situation. How animals deal with such internal conflicts has been, to a certain extent, investigated within another field of animal cognition research: the one concerned with behavioural indicators of metacognition. For instance, as will be revealed in the next section, in some of such studies, animals had to classify various items as equal to or different from a given benchmark (e.g., Smith et al., 1995). When these items were similar, but not equal to the benchmark, the animal would suffer an internal conflict, and, if possible, would opt out of the choice, or seek additional information. As the method introduced in this thesis should likewise spur internal conflicts in tested animals, it may be inspired by the methods that spurred such conflicts in so-called *uncertainty monitoring* studies.

Uncertainty monitoring

Most of the time, we scan the surroundings in search of something novel and unexpected that would draw our attention. During such scanning, we engage in a range of automatic behaviours. For instance, driving the car on our way to work, we stop at red lights, and wait till they go orange, and then green to start driving again. There is a different response associated with each light colour. Red means ”stop”, green means ”start”, orange means “get ready”. We can track these changes and react adequately while listening to the news or thinking about an upcoming meeting. Now, let us imagine that these signals are no longer clear-cut. There is only a single light, which gradually changes from red, through orange, to green, and back. Our “start” and “stop” responses will now require us to pay attention and judge whether the light is green enough to start, or red enough to stop (Smith, 2005). We would no longer be certain which shade of red is already orange enough to press the clutch pedal, and which shade of orange is green enough to release the clutch and press the gas.

People can monitor such feelings of uncertainty (Smith, 2005). In an uncertain situation, we defer a solution, and first engage in information-seeking behaviours: looking around, going back and forth, or getting closer to the source of difficulty in search of further perceptual information. That someone is feeling uncertain can be inferred from her non-verbal behaviour, but the uncertain person can also report this feeling: either verbally or non-verbally. Capability of reporting on own uncertainty can be tested in simple experimental setups. These setups consist of two basic components; on the one hand, they create a perceptual or cognitive difficulty for the participant, and, on the other, provide her with a behavioural response that allows her to report such difficulty (e.g., Smith, Shields, & Washburn, 2003).

Perceptual difficulties, such as discriminating between shades of colour, or sound and silence, were extensively studied in the 20th century. In a series of psychophysical experiments, people could respond “Uncertain” when they felt unable to classify task material into one of two primary classes, for instance “lighter than” and “heavier than” (Angell, 1907; Fernberger, 1914; 1930; George, 1917; Watson, Kellogg, Kawanishi, & Lucas, 1973; Woodworth, 1938). It usually took longer to issue the “Uncertain” response than to assign the presented items into one of the two classes (Angell, 1907; George, 1917; Woodworth, 1938), and issuing the “uncertain” response seemed to be more reflective and less automatic than the other one (Angell, 1907; Fernberger, 1930; George, 1917). Based on these observations, in 1990, Thomas O. Nelson and Louis Narens came up with an idea that cognitive processing could operate on two different levels: a lower “object” level and a higher “meta” level (Nelson & Narens, 1990). The meta-level, or metacognitive, processes were responsible for monitoring and managing the lower-level processes.

In other words, and according to Nelson Cowan’s model (1988, cf. Kanerva, 1988), cognitive processing could be carried out by two systems: the central executive and the memory system. The central executive would supervise, that is oversee and facilitate, processing of information from the memory system, and would, for instance, prioritise some inputs over the other, depending on the current needs of the individual. Thanks to these monitoring and control mechanisms, we can access and judge whether and how well we have acquired, are acquiring and could acquire certain information. In practice, we can make a range of judgements of own learning; we can, for instance, judge whether we already have some information (*feeling-of-knowing judgement*), how far we have progressed in acquiring the information (*judgement of achieved level of learning*), and how easily it could be acquired (*ease-of-learning judgement*). Making such judgements requires the use of our capacity for metacognition: taking stock of the ongoing cognitive processes (Smith et al., 2003). Because uncertainty monitoring relies on keeping track of decision-making and dealing with feelings of uncertainty when the decisions become difficult, it may indicate, according to some (Smith, 2005) but not others (Carruthers, 2008), such metacognitive level of cognitive processing. I do not attempt to take sides in the discussion on whether uncertainty monitoring requires a meta-level representation of own mental processes, or whether it relies solely on monitoring of own states, such as feelings of uncertainty. Regardless of this discussion, experimental setups used in uncertainty monitoring studies could inspire novel setups measuring the conflict-resolving ability, which is investigated in this thesis. However, I will come back to this discussion in the next section.

Uncertainty is associated with observable behaviours, which can be recognized as signs of hesitation: deferring a decisive action, and wavering between contradictory responses in the meantime, or opting for a response that produces a more certain, but potentially less rewarding, outcome. This means that, in principle, animal’s uncertainty could be inferred from such behaviours, if they were evinced by the animal put in a difficult situation. Showing behavioural signs of uncertainty would, in turn, suggest that the animal had access to uncertainty monitoring.

To induce feelings of uncertainty in the animal, one could simply combine the two above-mentioned rules: create a perceptual or cognitive difficulty and allow the animal to report it in its behaviour. This idea gave rise to a so-called comparative uncertainty-monitoring paradigm (Smith et al., 2003), which could be applied to various species and allowed studying animal self-awareness beyond the mirror-mark task (Gallup 1970, 1982; Gallup & Suarez, 1986). The mirror-mark task typically requires the animal to inspect a spot placed on its face or body, using the mirror reflection, but some, including Clayton and colleagues (1998), did not consider it a reliable test of self-awareness. The uncertainty-monitoring paradigm could offer an additional, perhaps more reliable, test of this capacity. Interestingly, the paradigm itself underwent similar shifts in a similar time-span as the mental-time-travelling paradigm; it started in 1995 with a simple setup derived from human psychophysical studies, was further developed in 2003 and 2005, and was later transformed to measure flexible adaptation to a dynamic environment.

Let us imagine that for any given shade from the spectrum between red and green, we must classify it as "red" or as "green", and otherwise report that we are "uncertain" to avoid the cost of a potential mistake. This was the task that J. David Smith and colleagues gave to five undergraduate students and a bottle-nosed dolphin in the first comparative uncertainty-monitoring setup (1995). Smith and colleagues used stimuli that were more relevant for a dolphin, namely a spectrum of tones. These tones should have been classified as high if equalled 2100 Hz and low if between 1200 and 2100 Hz. The dolphin (and the human participants in the analogical setup) was given three choices: it should have pressed a paddle located on the left wall of the pool if the tone was high, and another paddle located on the right wall, if the tone was low. Correct responses always led to praise and fish, but incorrect ones ended in a 9-s time-out. However, the dolphin was also given the third choice: it could press a third paddle, located on the back wall of the pool to refrain from making the "high"-"low" discrimination. Pressing the back paddle would discontinue the current trial and replace it with an easy low trial of 1200 Hz, which always led to a certain reward. The overuse of the third response increased the delays between pressing the third paddle and receiving the easy trial, so the animal had to use it sparingly to maintain the profitability of the "uncertain" response. Smith and colleagues found that both the students and the dolphin used this response in a similar way (1995): mostly for tones around 2070-2075 Hz, which were no longer low, but did not yet qualify as high. Therefore, both the students and the dolphin were uncertain of own responses in this range, and perhaps both could have monitored this state.

Two years later, Smith and colleagues used a similar setup to compare humans' and rhesus macaques' performance in the face of a perceptual difficulty (Smith, Shields, Shull, & Washburn, 1997; Shields, Smith, & Washburn, 1997), and soon their interest shifted to uncertainty induced by a memory difficulty (1998). In the latter setups, they introduced a so-called *serial probe recognition* task. In the serial probe recognition task, each participant first studied a list of four pictures, and afterwards had to decide whether a fifth picture was on the list or not. The participant could have chosen that the picture was "there", was "not there" or decline completing the task to avoid the cost of the failure. Interestingly, both the humans and the rhesus macaques declined the response most often in the area of maximum uncertainty, showed some individual differences in the response pattern, and performed better when they chose to complete the task than when they were forced to complete it by a lack of the "uncertain" response (Smith, Shields, Allendoerfer, & Washburn, 1998; Smith, 2005). Another experiment within this paradigm showed that the monkeys could, like humans, consult the strength of the available record and adjust the "uncertain" response accordingly. To show this ability, Hampton (2001) introduced a new version of a *delayed matching-to-sample* task (Elliott & Dolan, 1999; Etkin & D'Amato, 1969; Herman, 1975). In a classical delayed matching-to-sample task, the participant first is presented with a certain item, e.g., an image, and then, after a pre-specified interval, must choose this item from two or more items (for further information see *Working memory in animals*). In Hampton's version, this second presentation included the original sample and three other items. In every two out of three trials, the participant could either accept the choice, and engage in the task, or decline it. Declining led to a certain non-preferred food reward and no risk of time-out. Accepting could go both ways: if the choice was correct, it led to a preferred food reward, but if it was wrong, the participant was not allowed to engage in the task for some time. The interval between the initial presentation of the sample and the later presentation among the competitors was manipulated in one of the experimental conditions. If the participants indeed consulted the record strength, first, they should have been more likely to decline the choice as the delay got longer; second, they should have been more successful, when they were able to choose to engage in the task than when they were deprived of the "decline" response. One of the two monkeys indeed behaved this way, showing that it was able to keep track of the record strength, and adapt its strategy accordingly.

Two other issues were not, however, solved by these experiments. First, it remained unclear whether the animals' "uncertain" response was rather reflective than automatic, like it was in the case of humans (Angell, 1907; George, 1917). Second, so far, the animals were trained to use this response in static environments which could foster inflexible and conditioned responses (Zakrzewski, Perdue, Beran, Church, & Smith, 2014). The first question was tackled by Smith and colleagues, who used a similar setup as in the dolphin experiment (2013). They expected that classifying the sample as belonging to a clear-cut category would be less affected by participating in another simultaneous and cognitively demanding task than issuing the "uncertain" response. To test whether this was the case, Smith and colleagues added a fourth choice: a "middle" one. It was associated with the same part of the spectrum that posed the perceptual difficulty and led to the “uncertain” response. In each trial, rhesus macaques would see a square pixel box that was filled with a number of randomly located white pixels against a black background (Smith, Coutinho, Church, & Beran, 2013). The density of the pixels was picked from a spectrum from sparse to dense. Accordingly, all monkeys could decide whether the pixel distribution in a given trial was “sparse” or “dense”. However, some monkeys learned that distributions between these two extremes could be classified as “middle”, and others were not trained on this category, having the access to the “uncertain” response instead. In between the “sparse”-“dense” trials, the monkeys from both groups participated in a simple short-term memory task (matching-to-sample) to suffer an additional load on cognitive processing of the main task. Smith and colleagues found that the monkeys in the “uncertain” group performed worse with the concurrent load than the monkeys in the “middle” group, suggesting that the “uncertain” response was perhaps more dependent on the central executive and/or required more attentional resources than more automatic and more perceptually-driven responses. Therefore, it seemed that the “uncertain” response may have a similarly reflective character in the rhesus macaques as in the humans.

The second issue – of whether animals could flexibly adjust the “uncertain” response to a dynamically changing environment – was addressed by Zakrzewski and colleagues (2014) in a slightly different experimental setup. This time, humans and rhesus macaques again judged whether the pixel-filled rectangle had a “sparse” or a “dense” distribution of the pixels, but the simple “uncertain” response was replaced with a “cash-out”. Here, the rectangle was presented on a screen along with an additional box, in which, after each correct answer, a gold coin would appear. The participants could have gathered up to eight coins in the box if they correctly answered eight trials in a row; however, upon any wrong answer, the coins would disappear, and the participants would lose all potential rewards accumulated up to that point. Even if the participants were uncertain of own response, they could not decline any trials in this setup. Instead, they were given a cash-out response to manage the risk associated with the accumulated rewards and uncertainty of the correct answer. They could have chosen to cash out at any trial; upon cashing-out, the macaques would receive as many pellets and the humans as many points, as the coin number was at that moment. To prevent cashing out after each correct response, choosing the cash-out was followed by a temporary inaccessibility of the task, lasting 20 seconds for the humans and 8 seconds for the monkeys. Such a token-bank system allowed participants to, on the one hand, keep track how much was at risk, and on the other, to withdraw the accumulated rewards when the outcome of the trial seemed too uncertain. Because the participants had to complete the test after withdrawal anyway, the experimenter could track the relationship between withdrawals and failures on the withdrawn-from trials. Interestingly, both the macaques and the humans flexibly adjusted their decisions to balance the cost of error against the trail difficulty and the number of rewards at risk (Zakrzewski et al., 2014). Both groups were the more likely to use the cash-out response, the more rewards were at risk, and, in both, the participants gave answers adjusted to the task at hand, flexibly changing own strategy on trial-by-trial basis. Admittedly, there was a difference between the two groups: in the trials, in which high numbers of rewards were at stake, the humans used the cash-out response more rarely than the macaques. This effect was, however, previously found in other uncertainty studies with humans, suggesting that human performance can fall prey to a so-called overconfidence effect (Galotti, 2008), or associating uncertainty with mental weakness (Smith, Beran, & Couchman, 2012), and not pleading "uncertain" even if one is uncertain of own answers. Therefore, the macaques were more likely to cash out when the risk of losing the rewards was high than the humans. This means that they could have monitored both this risk and own uncertainty of the correct answer, and so showed a human-like flexibility in decision-making in the face of uncertainty.

The last two examples of experimental setups – by Smith and colleagues (2013) and Zakrzewski and colleagues (2014) – had something in common with all setups described under the umbrella-term of comparative uncertainty-monitoring paradigm: they posed a difficulty for the participants. This difficulty, or conflict, had to be resolved on the basis of previous knowledge and the currently available perceptual information, but required a certain degree of creativity. Although the situation at hand partially overlapped with different records of the past, there was no perfect match. On top of that, the imperfect matches were previously resolved with various, sometimes even contradictory, behavioural responses, such as pressing the left vs. the right paddle, or moving the cursor to "S" for the "sparse" vs. "D" for the "dense" distribution of the pixels.

The uncertainty-monitoring experimental setups involve a simplified version of everyday challenges, as both animals and humans encounter situations, in which automatic behavioural responses are thwarted, leading to the state of uncertainty. "Difficulty and uncertainty imply that the well-learned behaviour, the well-oiled habit, will not work and could be dangerous" (Smith, 2005, p. 28). Therefore, when records of the past situation map inconsistently and unreliably onto the current behavioural responses, a cognitive higher instance has to step in and adjudicate on the conflict (Shiffrin & Schneider, 1977). In fact, such conflicts - between goals and behavioural responses - drew a lot of attention in psychology (James, 1890; Tolman, 1932; Karoly, 1993; Gray, 1995). Cognitively challenging situations were supposed to induce a unique state that required the metacognitive level of processing. This level received different names over the years; William James wrote about "agonizingly intense consciousness" (1890, p. 142), Edward C. Tolman about "conscious awareness" (1967, p. 217), Paul Karoly about "self-regulation" (1993, p. 25), and Jeffrey A. Gray about "special neural circuits that may arrest behaviour, increase arousal, and redirect attention and mental resources toward the causes of difficulty" (1995; after Smith, 2005, p. 27).

Inducing conflicts between goals and responses seems, therefore, to be a promising way of testing the metacognitive level of processing in animals. If one wants to test whether and how the animal deals with a cognitively difficult problem, one needs to create a conflict between at least two different responses and either give the animal an opt-out response (“uncertain” or “cash-out”), and/or keep track of changes in its behaviour between the presentation and an attempt at the resolution. In the first study from 1995, the dolphin did both – pressed one of the paddles on the one hand, and swam back and forth, slowed down and wavered between the paddles on the other – but only pressing the paddles was a part of the experimental design. Because the changes in behaviour were, at least by some (Goldsmith & Koriat, 2003), considered more convincing than the paddle-pressing response, tracking such changes within an experimental setup could become a more convincing measure of conflict resolution and the use of metacognition on the animal’s part.

Metarepresentation

Zakrzewski and colleagues (2014) showed that the rhesus macaques were aware of the risks associated with the task and could flexibly use it to own advantage. Their performance in the task required monitoring the internal uncertainty and the external magnitude of the reward. However, it is unclear whether the macaques monitored own feelings of uncertainty against the risk of losing the reward, or whether they could not reliably compare some of the current sample against an internally represented spectrum of samples. Simply put, it is unclear whether the animals consulted the “hunch” of uncertainty or referred to so-called metarepresentation. As Peter Carruthers and J. Brendan Ritchie put it (2012), the animals could rely on non-metarepresentational uses of feelings of uncertainty. Before moving any further, we must consider what *metarepresentation* is and how it relates to *metacognition*.

The term of *metacognition* could be defined in at least two ways; it can refer to the *self-evaluative function* of cognitive processing, which supports the monitoring and the control of ongoing activities; alternatively, it can refer to the *self-ascriptive function* of cognitive processing, which operates on representations of own mental states as mental states (Proust, 2012). As mentioned above, only one of these definitions qualifies uncertainty monitoring as metacognitive. This definition, used by Smith and colleagues (2003) and Couchman and colleagues (2012), assumes that one can have access to metacognition without the access to metarepresentations, that is, representations about own mental states. For instance, if one can monitor the feedback, e.g., feelings of uncertainty, generated in the body while engaging in a simple cognitive task, and adjust own behavioural responses accordingly, one is endowed with a certain level of metacognition. In other words, the capacity for monitoring of own affective and mental states is considered a metacognitive one. This means that, according to this view, metacognition is a spectrum of cognitive capacities which may be situated anywhere between monitoring and metarepresentation (Couchman, Beran, Coutinho, & Smith, 2012). This view is not shared by, among others, Carruthers (2008, 2009) and Crystal (2012), who postulate that metacognitive level of processing necessarily requires and operates on metarepresentations. In this self-ascriptive view, the access to metacognition is not possible without the access to metarepresentations. One cannot select and monitor own cognitive activities unless one can represent that one has mental states with specific contents (Proust, 2012). And, to represent own mental states as mental states, one needs two levels of representation: a primary and a secondary one. When one encounters a certain stimulus in the world or in oneself, one creates a primary internal representation of this stimulus (Crystal, 2012), which allows for expanding or updating the internal model of the world. The stimulus can come from an item, an affective state (e.g., a feeling) or a mental state (e.g., belief), and allows for noticing than one is encountering the given item or is in the given, affective or mental, state. However, in principle, one can act upon such primary representations without knowing that one encounters the given item, or is in the given state. One can simply engage in an action that is appropriate when the item or the state is detected, without creating a secondary representation, that is, a representation about knowledge of encountering the item or being in the state. According to the self-ascriptive view, creating such secondary representations, that is metarepresentations, is a necessary criterion of metacognition.

The capacity for metarepresentation, understood as secondary representation, could widen the gap between the human and the animal capacity for mental-time-travelling (Redshaw, 2014). This idea was put forward by Jonathan Redshaw in response to the finding that, according to Michael C. Corballis (2013), strengthened the case of evolutionary continuity of mental time travelling. Between 2006 and 2010, several teams of researchers found that rats could not only mentally represent familiar routes an earlier-visited maze and replay them forward and backward (Foster & Wilson, 2006), but could also represent novel routes (Gupta, van der Meer, Touretzky, & Redish, 2010) and were more likely to follow them in the future (Pfeiffer & Foster, 2013; Redshaw, 2014). These findings suggested that at least rats could use the already-mentioned default mode network to generate mental representations of alternative versions of reality. However, the animals could, as Redshaw put it (2014), lack the understanding of the relation between these representations and reality; that is, the animals did not need to understand that the current reality existed independently of their mind and that they could compare the representations of “how things were” to “how things are now”. According to Redshaw, this understanding was uniquely available to humans who could “embed alternative representations of reality within a specific representational context – whether that context be another mind, the past, the future, or mere fiction – and relate these representations to a continuously updating model of current reality" (2014, p. 520). Animals, on the other hand, could only form uncontextualized representations that would pertain to evolutionarily recurrent themes, such as spatial trajectories or potential survival threats, or random recombinations of stored records of the past. Therefore, the animals, contrary to the humans, could not understand the relation between the record of the past and the view of the current situation and could not use the records of the past to exert purposeful constructive control over the stored records. They could come up with novel alternative scenarios of what happened and could happen, but could not generate such scenarios on purpose to deal with a difficult situation at hand.

The metarepresentational gap between the animals' and the humans' cognitive capacities seemed to come, again, from an absence of evidence and not an evidence of absence. But, in principle, one could perhaps design an experimental setup that would allow for testing whether this gap actually exists. This task is tricky because comparing the "now" against the "past" or the "future", or comparing two "pasts", or two "futures" with each other may, but does not need to, require the capacity for metarepresentation. Such comparisons can be based on first-order representations and misrepresentations of the "now", the "past" and the "future", treated as currently available affective or mental states. However, these comparisons may also be based on metarepresentations of such states, if one knows that representations and misrepresentations of the "now", the "past" and the "future" are indeed representations about own affective or mental states.

Making decisions in the face of conflicting perceptual information does not allow for testing whether the participant is capable of metarepresentation because it does not require comparing the situation at hand against a record of another reality. That is only possible if the task relies on a conflict between how the reality is now and how it seems to be (cf. Carruthers, 2008). Therefore, it requires creating a conflict between a current representation of the reality and a misrepresentation of this reality, spurred by a past reality that looked the same yet was not. Using such conflicts between appearance and reality allowed for establishing that children before 4-5 years of age, that is, before the hypothesised onset of episodic memory and episodic foresight (e.g., Lee, 2012), have difficulties in discerning between the perceptual appearance and the real properties of same-looking items (Flavell, Flavell, & Green 1983; Flavell, Green, Flavell, Watson, & Campione, 1986; Moll & Tomasello, 2012; Proust, 2012). In other words, they have difficulties in discerning between how the reality is now and how it seems to be, which shows that, at least in humans, the development of metarepresentation might coincide with the development of episodic memory. As both metarepresentation and episodic memory were related to human mental time travelling, creating similar conflicts could perhaps allow for testing the overlap between these capacities in animals.

In an experimental setup that would operate on the conflict between a current representation of the reality and a misrepresentation of this reality, one must be confronted with a problem that looks like another problem encountered in the past, but in fact requires a retrieval of another problem that had a similar solution. If the animal can realise that the representation of the past is actually a misrepresentation of the present, it should be able to move away from this misrepresentation and search for another record that may contain the relevant solution.

In this thesis, I am especially interested in creating this conflict. The participant should be initially cued to the representation that is perceptually overlapping with the situation at hand. Being cued to that representation should result in a currently incorrect behavioural response associated with that representation. Once this response proves to be unproductive, the participant should be able to select another representation that is not perceptually overlapping with the situation at hand, but potentially contains information that is more relevant in the current situation. Whether the setup introduced in this thesis could allow for concurrent testing of metarepresentation and episodic memory, either in the present form or after certain modifications, remains open.

It seems that the two decades of mental-time-travelling and uncertainty-monitoring paradigms offer multiple clues as to what such a setup could consist of. The first clue relates to the question of flexibility: in both paradigms, after a series of static experiments, the researchers shifted their interest to dynamic environments, in which the animal had to draw on previous experiences in the face of a never-experienced challenge. The second clue points to inducing a conflict between records of the past and the current reality. And the third, and final, clue suggests that one needs to track the animal's behaviour between the presentation of the conflict and the eventual conflict resolution. How could all these clues come together in a non-verbal experimental setup? The answer can, perhaps unexpectedly, be derived from experimental setups used in another field of research: the field of computer modelling.

AMBR and DUAL

In 1988, the year in which Pentti Kanerva published his book on sparse distributed memory, Boicho Kokinov introduced another model: of so-called *Associative Memory-Based Reasoning* (from now on: AMBR; Kokinov, 1988a, 1988b). The AMBR modelled processes behind problem-solving and, contrary to most of the models at that time, accounted for many malfunctions of human memory. The aim of the AMBR was the same as Kanerva's: to model how memory worked in everyday life. It aimed to accommodate a wide range of empirical findings from human memory research, and to generate predictions that could be tested in relatively simple experimental setups. The setups used by Kokinov and colleagues (Kokinov, 1990; Kokinov & Zareva-Toncheva, 2001; Zareva-Toncheva &

Kokinov, 2003; Petkov & Kokinov, 2009; Pavlova & Kokinov, 2014) directly inspired a setup that, at least to some extent, accommodated the three above-mentioned clues and was tested with great apes and Goffin's cockatoos within the scope of this thesis (see Papers I-II).

Because information processing requires a cognitive architecture that would carry it out, AMBR also requires such architecture, called DUAL. DUAL is a network of units, similar to a neural network, which carries out cognitive processing gathered under an umbrella-term of the AMBR (Kokinov & Petrov, 2001). The AMBR consists of a set of parallel processes, such as retrieving, mapping, transferring, evaluating and updating, that operate on a network of traces (Kokinov & Zareva-Toncheva, 2001). Each trace carries a piece of information about a certain item: object, concept, rule, fact, or episode. The trace is not a stable tangible entity waiting for retrieval in the memory store, but a temporary state constructed on the spot from the information available in the system (Kokinov & Petrov, 2001). Therefore, memory itself is not a physical space, in which items are stored as static structures waiting for future retrieval, but is considered a constructive process instead (Bartlett, 1932; Neisser, 1981; Brewer, 1988; Schacter, 1995).

In the AMBR, the traces can be reconstructed upon the cue. Which traces will participate in this reconstruction is determined by the context formed by three types of input: (1) the perceptual input from the current environment, (2) the input from the internal model of the world, and (3) the current state of the system, that is, the accessibility of specific information at a given moment. This accessibility depends on the current activation of the traces: more active traces are more accessible and have more impact on the outcome of processing than less active traces. Which traces have been activated in an immediately past situation will influence the activation of the new traces and, thereby, the behavioural response to the current situation. In other words, what we do before tackling a specific task, influences our performance in the task. This is intuitive; for instance, writing a letter feels different after reading a book than after making calculations, and driving a rental car feels different after driving another car than after reading a book. Activation of some specific knowledge and/or skills before a given problem, was found to influence the way in which we approach it and whether we solve it or not (Kokinov, 1990). This effect, known as *priming*, has been extensively investigated in humans (e.g., Tulving & Schacter, 1990; Roediger & McDermott, 1993; Mulligan, 1996), and was tested in some experimental setups within the AMBR, described at the end of this section.

The outcome of our behaviour depends on the context, because the context of retrieval affects which information is activated, accessed and retrieved. To simulate cognitive processing that incorporates this idea, one needs to simulate the links between context, activation and accessibility. First, the current context must influence what is activated. Second, what becomes more activated must also become more accessible. Third, the simulation of the first two relations must allow for flexible processing of dynamic and unpredictable contexts. These three relations are incorporated into the AMBR model and supported by the DUAL network. However, to understand how they operate in practice, we need to understand how the network itself works first.

The network consists of basic computational units called *agents*. A single agent can be responsible for a piece of information about a concept, an object or an episode (Kokinov & Petrov, 2001), but neither of the agents has all the information that the system has about these items. Like in Kanerva's model, the record is split into traces, and each trace is distributed over a set of agents. Such agents are connected to each other and form so-called *coalitions*. The coalitions usually consist of more-or-less stable set of agents, but they are not fixed in advance. This means that each time the activation spreads in the network, the coalitions are formed dynamically as the agents establish the mutual links anew (Kokinov & Petrov, 2001). Whenever the activation of the agents exceeds a certain threshold, they form a *working memory* of the system. The most active agents within working memory will form a *focus*. It is noteworthy that both the working memory and the focus can concurrently include agents from different coalitions, which contain information relevant enough for the problem at hand. This allows for the above-mentioned combinatorial flexibility, that is, combining traces that initially belonged to different records in a novel way.

Taking notes and using them in the future could serve as a good example of how coalitions work. When we take notes, we usually have a series of sentences grouped source-by-source, e.g., coming from two different books. The sentences written by the first author are internally linked to each other, as are the sentences that come from the second author. Each sentence is like an agent; and the group of sentences from a single book is like a coalition. The sentences are undeniably linked to each other because they share the same author. But they can also be linked to sentences that come from another author, if, for instance, they contain different pieces of information related to the same topic. Now, if we want to find out what one of these authors said about a certain topic, we will need the sentences – the agents – to form a coalition similar to the initial one; but if we want to know how the topic is addressed by both authors, we will need to rearrange the agents into another coalition, more fit for this purpose. This is how the context of retrieval shapes the currently available coalitions.

How is it possible in the DUAL architecture? We have already established that accessing agents and provoking them to form coalitions relies on their activation. This activation reaches different areas of the network by a spreading activation mechanism, which can be directed or automatic (Kokinov, 1990). The directed spreading is performed when some pieces of information are directly sought after in response to a certain cue, whereas the automatic spreading is performed continuously, and parallels all other processes carried out within the network. The activation is spread through links from one agent to another. The level of activation determines how accessible the agent becomes: as the agent becomes more active, the associated piece of information becomes more accessible, and is considered more relevant for the current context. Thanks to these operations, the AMBR can model how the changes in the context lead to differences in accessibility of different traces, and, as a result, different behavioural outcomes. However, dealing with dynamically changing contexts is solved in a slightly different way: with an ability of setting up temporary links and agents.

Each agent has a dual function: on the one hand, it can establish links with the neighbouring agents, and on the other, it can interact with them. The links and the interactions are possible only when the agent's activation level exceeds a certain threshold. A majority of agents and links comes from records of the past experiences and, therefore, is permanently available in the system. Each permanent agent can pass signals to other agents with a speed proportional to its activation level. However, not all agents are equal. In a majority of the coalitions, such as those responsible for concepts and objects, there is a leader agent that contains a list of frequent coalition members. The leader agents play a crucial role in setting up temporary agents and links, as they can emit a special type of signal. Whenever the activation of the leader agent exceeds the threshold, it sends out a signal that the item encoded in its coalition has been detected. And once this item is detected at least twice, for instance, once in the perceptual input and once in the memory traces, the system assumes that an item, similar to the previously encountered one, is currently available in the environment. The hypothesized similarity between these items becomes a separate temporary agent. If this hypothesis is not rejected, the agent will become a permanent one; if the hypothesis is rejected, the agent will vanish from the network. Setting up such temporary agents supports a dynamic predict-implement-update-predict loop in unpredictable situations, and, therefore, facilitates adaptive responses to dynamically changing contexts.

The AMBR simulates how memory works without distinguishing between the declarative and the procedural knowledge, but it accounts for two other distinctions between memory processes, discussed in psychological research: (1) between the long-term memory and the working memory, and (2) between the semantic memory and the episodic memory. (1) All agents, regardless of the current activity level, belong to the *long-term memory* of the system. The agents, whose activation at a given moment exceeds the above-mentioned threshold, form together the *working memory* of the system, and the most active agents form the *focus*. It is perhaps worth noting that the term of *focus* was also used in Kanerva's model, but had a different meaning; working memory and attention (focus) will be discussed below in the section on *Attention*. (2) Furthermore, the AMBR accommodates Tulving's distinction between the semantic and the episodic memory, and explains why the episodic memory system might be more useful but malleable dynamic context changes. Although many coalitions have the leader agents, this is true only for those coalitions that refer to items of semantic knowledge: e.g., objects and facts, as only these items tend to have a name that can be associated with the leader ("favourite song", "World War II"). This is not the case for episodes, that are typically more complex and unique, and therefore do not have a specific name which could be associated with the leader. Because the traces of episodes lack such leader agents, they are more decentralized and distributed in the network than the traces of objects or facts, and, therefore, are less stable and more susceptible to the current context (Kokinov & Petrov, 2001).

Context-sensitive and flexible retrieval is key for the constructive character of memory as we have already seen in the first part of the introduction, and it seems that there is a way of accounting for this flexibility in the AMBR model. The model does not assume that our memory is perfectly accurate; it assumes that accuracy can be sacrificed, whenever flexibility is at stake. The inaccuracies of our memory are driven by the same processes of mapping and retrieval that drive memory flexibility (e.g., Petkov & Kokinov, 2009). According to the model, remembering is an active process of interpreting the available traces, just like visual perception is an active process of interpreting the available visual information (Neisser, 1967). Upon the cue, a new episode is constructed from the distributed traces; this new trace should be as similar as possible to the original episode, but often is rather a hybrid interpretation of several relevant past episodes. In this process, different hypotheses are constructed as to what happened in the original episode, and these hypotheses are systematically rejected, one after another, in a series of activation changes. Because only the most active and the most relevant agents will enter the working memory, only few most plausible hypotheses will influence the actual behavioural outcome of the process. According to the model, such hypotheses-testing and the active construction of the episode allow greater flexibility, but leaves room for memory malfunctions.

Problems after problems

Those who agree that memory is a constructive process ask different questions than those that perceive it as a store (Kokinov & Petrov, 2001). Instead of using simple artificial testing material, such as series of words, numbers or pictures and testing whether the participant remembers something or not, the proponents of the constructive view study memory in more natural settings (e.g., Dunbar, 2001; Kokinov & Petrov, 2001). Instead of testing how well someone recalls the to-be-remembered material, they test what use someone makes of whatever she remembers, and how the context affects her performance. These two latter questions gave rise to Kokinov and colleagues' interest in simple experimental setups that required problem-solving (e.g., Kokinov, 1990; Kokinov & Zareva-Toncheva, 2001; Zareva-Toncheva & Kokinov, 2003; Petkov & Kokinov, 2009). In a typical setup, participants received a series of simple problems, such as mathematical equations, short stories, geometry tasks and other. The experimenter recorded how the participants dealt with the problems after dealing with other, similar, dissimilar, or unrelated ones. For instance, in a priming experiment from 1990, each participant tackled a certain target problem and belonged to one of three groups: control, near-priming and far-priming (Kokinov, 1990). What the participants did before tackling the target problem, differed between the groups. They solved an unrelated problem in the control, a related problem in the near-priming, and a related problem followed by two unrelated ones in the far-priming. The target problem was, for instance: “Imagine a spring with a weight hung on it; if the original spring is replaced with one made of the same kind of wire, with the same number of coils, but with coils twice as wide in diameter, will the spring now stretch more, less, or the same amount under the same weight, and why?” (Kokinov, 1990). The related problem went as follows: “There are two rods made of one and the same material with the same width and profile, but with different lengths. Each rod is fixed horizontally by one of its ends and a weight (the same for both rods) is hung at the other end. Which rod will bend more?” (Kokinov, 1990). Mathematic equations and geometry tasks served as the unrelated problems.

Obviously, this experimental setup cannot be directly translated into a non-verbal comparative behavioural study. However, the first principle behind Kokinov and colleagues’ efforts can be tied to the three above-mentioned clues. The principle is: we never solve a newly encountered problem in a void, and solving similar problems beforehand changes the way, in which we tackle the current one. This principle has been implemented in so-called *transfer* studies in animal cognition research, but it has usually served testing causal understanding rather than memory. Let us have a brief look at those studies, as they tend to show how one deals with a given problem after solving another, related and helpful, one.

Transfer studies in animals

Solving some problems may improve our chance of solving other, somewhat similar, ones. But could any animal benefit from such an improvement? This question has been repeatedly addressed in the last 25 years, since Elisabetta Visalberghi and Luca Limongelli introduced a so-called trap-tube task (Visalberghi & Limongelli, 1994; Martin-Ordas, Call, & Colmenares, 2008). In this task, capuchin monkeys, first, learned how to push a reward out of a transparent hollow Plexiglas tube with a stick. Once the animals mastered this task, they were confronted with a same-looking tube with a hole in the middle, through which the reward, if pushed from the wrong side, would drop and disappear in a trap. In the first tube, it did not matter through which side opening the stick was inserted and pushed. However, in the second tube, the choice of the opening could have had grave consequences. If the stick was inserted through the opening closer to the food item and pushed, the reward would fall into the trap. Therefore, to avoid losing the reward, the monkey had to insert the stick through the more distant opening and, only then, push the reward out of the tube. The monkey should have used this second strategy, and so avoid pushing the item into the trap, if it understood the causal relationships that governed the task. Three out of four monkeys did not perform too well, and only the fourth learned to solve the task over time. However, most likely, this monkey just learned that it needed to push the stick through the more distant opening rather than the causal relationships that governed the task.

This task gave rise to a variety of different-looking trap tasks: tubes, tables and platforms, all of which shared the same principle: animals had to obtain the reward by avoiding a built-in trap (Martin-Ordas & Call, 2009). Although these tasks followed a similar idea as Kokinov's (1990), that is, introduced a series of tasks that should have improved the participant's performance in the test task, they were not used to study animal memory. They served another purpose instead: of testing, to what extent animals could understand causal relationships that governed a given task and transfer this understanding across different looking but functionally overlapping tasks. Two tasks were typically considered functionally overlapping, if they shared the same principle for solution: in this case, avoiding the trap. In such experimental setups, other trap tasks had to accompany the trap-tube task. For this reason, trap-table and trap-platform tasks were conceived (Martin-Ordas et al., 2008). The trap-table was first used by Daniel Povinelli to test causal understanding in chimpanzees (2000) and consisted of two sections: a left and a right one, separated by a partition wall. Each table came with a reward located in the back of the table, and a tool that allowed for raking the reward toward the front. Although both table sections shared all these elements, there was a substantial difference between them: one of the sections had a cut-out hole on the reward's way. If the animal chose to rake the reward located in the back of this section, the reward would fall and disappear into the trap. This task was later transformed by Gema Martin-Ordas and colleagues (2008) into a trap-platform that consisted of two L-shaped elements, forming together a U-shaped platform. The two arms of the apparatus were directly adjacent to the animal's cage. As the reward was in the middle of the platform, the animal had to push the reward to the left or to the right, and then rake to the front. However, just like in the trap-table, one of the L-shaped sections had a cut-out hole on the reward's way. If the reward was pushed to that side, it would fall and disappear into the trap.

The original trap-tube task likewise underwent some transformations over the years (Mulcahy & Call, 2006b; Seed, Tebbich, Emery, & Clayton, 2006; Taylor, Hunt, Medina, & Gray, 2009), as it was adjusted to the sensorimotor skills and preferences of the tested species. For instance, Nicholas J. Mulcahy and Josep Call modified the setup to account for the preference for raking over pushing the rewards in great apes (2006b), and Amanda Seed and colleagues adjusted it to non-tool-using rooks (2006). Overall, only some animals were capable of transferring between the different looking, yet functionally overlapping tasks. Great apes, such as orangutans, chimpanzees, bonobos and gorillas, showed neither transfer between a trap-tube and a trap-platform in 2008 (Martin-Ordas et al., 2008), nor between a trap-platform and other trap-tasks in 2009 (Martin-Ordas & Call, 2009). However, the apes seemed to transfer between a trap-tube and a trap-table (Martin-Ordas & Call, 2009). In a similar vein, New Caledonian crows were capable of transfer between a trap-tube and a trap table (Taylor et al., 2009), and rooks (Seed et al. 2006) were also found to transfer across some trap-tube setups.

In general, the trap-task studies focused on two questions: (1) how well animals understood the causal relationships that governed the task (Seed et al., 2006), or (2) whether animals could use knowledge obtained in one task in another, different looking task (Taylor et al., 2009). While using traps could be informative about the first question, it could lead to an unclear and/or misleading answer to the second. A negative result, that is the lack of transfer across the trap tasks, could have said more about the task itself, rather than the species' cognitive capacities. This is of course true for all tasks designed for animals, but the trap tasks seemed to be especially problematic. Poor performance on a trap task could have resulted from physical limitations on the task's and noncognitive limitations on the animal's part. First and foremost, the above-mentioned setups had only one thing in common: if the animal executed certain motor actions, the reward would disappear into a trap. While such disappearing into a trap might be a sufficient criterion of functional overlap for an adult human experimenter, it might not be perceived as such by the tested animals. Second, the trap tasks limited the behavioural repertoire of the tested animals and did not leave much space for flexible behaviours. Both when the trap tasks required tool use, which posed an additional difficulty, even to tool-using animals (Seed, Call, Emey, & Clayton, 2009a), and when they required simple movements, such as pulling a rod (Seed et al., 2006), the pool of correct motor responses was very limited. Third, as we have already learned, some of the tasks were not adjusted to the animals' preferences, and therefore, led to failures that revealed more about preferences for certain motor actions than causal understanding. Last, but not least, it is difficult to assess whether the animals would experience losing a food item to a trap in their natural environments.

The question of whether animals could transfer knowledge across different looking tasks, was also tackled by other, non-trap experimental setups. In some of those setups, cotton-top tamarins would distinguish functionally relevant features of the task from the irrelevant, and transfer across simple tasks (Hauser 1997, 1999); Goffin's cockatoos would flexibly adjust own responses to various configurations of locks (Auersperg, Kacelnik, & Bayern, 2013); and red-shouldered macaws, along with black-headed caiques, could transfer across problems that required attending to the size of gaps and objects that were supposed to pass through those gaps (van Horik & Emery, 2016). However, none of these tasks was used to test whether animals could transfer knowledge across different-looking problems after a delay, using long-term memory. This question was addressed only in 2012, as Gill L. Vale and colleagues retested chimpanzees on a familiar tool-use task from 2008, and then confronted them with another, functionally overlapping task (Vale et al., 2016). In the original task, the chimpanzees were supposed to obtain a grape, available in one of two locations – a closer or a more distant one – using the available toolkit. The toolkit consisted of a 28 cm rod and a 39 cm hollow polycarbonate tube, and, in this form, allowed only for the retrieval of the closer rewards. To reach the more distant rewards, the chimpanzees had to obtain a longer tool by combining the rod and the tube. This procedure was carried out in 2008 and the chimpanzees had no access to the setup until 2012. In 2012, they received the task again, and not only retained the previously used tool-combining techniques but were also faster in obtaining the rewards. Once the chimpanzees completed the familiar task, they proceeded to another task, in which they received the same toolkit. The new task consisted of a box with two openings in the front and two protruding tubes on the top. In each trial, one of the tubes was filled with a bunch of grapes. Each opening contained a sliding mechanism that, if pushed, would release the grapes from these tubes. However, again, the sliding mechanism in one of the openings was closer, and the other was more distant, so that pushing the more distant one required the combined tool. The chimpanzees were, again, able to combine the tools and use them effectively in this task, using a skill that was first acquired three years and seven months earlier.

However, retesting the chimpanzees in 2012 on the familiar task slightly blurred the result in the transfer task. The chimpanzees certainly transferred between the two functionally overlapping tasks, but would they be able to do so without the retest? Only solving the unfamiliar task without the retest would suggest that the chimpanzees retrieved a record of the familiar task from episodic memory. Even if they were able to succeed without the retest, the result would reveal that the tested chimpanzees, like scrub jays (Clayton et al., 2001) and other great apes (Osvath & Osvath, 2008), were capable of using relevant, previously acquired, information in a different-looking situation. However, the success would not reveal that the chimpanzees had access to memory flexibility, investigated in this thesis. Such flexibility would require extracting different pieces of information from at least two records of the past and putting them together to resolve a certain problem at hand. If any animal could do just that, it should use this ability to own advantage. In other words, if the animal solved two helpful problems, each of which could inform the current solution, it should be able to extract the relevant pieces of information out of those problems and apply them to the current context. However, this ability should also have a downside: if any of these problems only seems to be relevant, but in fact is misleading and irrelevant, the animal should suffer a conflict between the relevant and the irrelevant information. If the animal has a relevant and an irrelevant record in long-term memory, it should be hindered by the irrelevant record until the conflict between these records is resolved. Therefore, in an experimental setup that could address this issue, the animal must be confronted with a problem that would partially overlap with both the relevant and the irrelevant record, acquired in the past. Preferably, the irrelevant record should falsely represent the current reality, and the relevant record should have little to do with the current reality at first glance. For instance, the irrelevant record could overlap perceptually with the current problem. Such perceptual overlap would result in an immediate cueing to the irrelevant record, which would be associated with a stronger feeling of accuracy and falsely represent (misrepresent) the current reality. The other record should contain information on the correct solution of the problem at hand, so, in other words, it must overlap functionally with the current problem.

Creating a conflict

None of the above-mentioned transfer tasks tested what would happen, if solving a related and helpful problem was followed by a related yet hindering one. This could be a good way of testing whether any animal had access to combinatorial flexibility. If this was the case, they should be able to select the relevant helpful problem over the hindering one and use it to resolve a novel problem at hand. Creating an experimental setup that would allow for investigating this question requires tying the three clues derived from the mental-time-travelling and uncertainty-monitoring paradigms and two clues derived from Kokinov and colleagues' experiments. The three clues were as follows: (1) in the test, an animal must receive a never-encountered problem, (2) in the test, one must create a conflict/a difficulty for the animal, (3) in the test, one must track the changes in the animal's behaviour after the presentation of the conflict until the animal solves or abandons it. The two further clues from Kokinov and colleagues' experiments are as follows: (4) one must use a setup that involves problem-solving, (5) previously solved and related problems influence, that is, enhance or hinder, solving the current problem.

Therefore, in a simplest possible setup, one needs to create a conflict between two problems solved in the past, both of which would somewhat overlap with the test problem at hand. For instance, the conflict between the problems could come from solving two related problems beforehand: one that would facilitate, and another that would hinder solving the test problem. If the first problem should facilitate solving the test, it could overlap functionally, as then the motor action that led to solving that problem would lead to solving the test. And if the second problem should hinder solving the test problem, it must be solved with another motor action, but as it must be also somehow related to the test problem, it must look more-or-less the same (overlap perceptually) as the test problem. This is how one could implement the fourth clue in a non-verbal experimental setup. However, in such a setup, the test problem could not be completely new; after all, the animal might be able to solve the problem spontaneously without any help. Therefore, one must first make sure that the animal could not solve the problem spontaneously by presenting the animal with the test problem at the beginning of the experiment. One could not fully implement the first clue, but instead, one could test how the animal would perform on the same test problem after a delay, without solving any problems – neither helpful, not hindering – before another exposure to the same test problem. If the animal managed to solve the test problem upon the second exposure, we could not say that any problems in between were prerequisite for succeeding in the test. This conclusion would only be right, if the animal could not succeed without any training. Regardless of the outcome, one could record how the animal behaved and what it did until solving, or abandoning the problem, or declining further participation. Afterwards, based on the recording, one could code how much time the animal spent on interactions with specific components of the problem, and thereby obtain a continuous measure of behavioural changes throughout the performance, in accordance with the third clue.

To implement the rest of the clues, that is, the second and the fifth, one would need to introduce some problems before the second presentation of the target problem. Specifically, first, one should teach the animal how to solve a functionally overlapping problem, and only then how to solve another, perceptually overlapping, problem. This is how one would create the conflict for the animal: upon the second presentation of the test problem, it should be cued to the solution of the perceptually overlapping problem, which, however, would not allow for solving the current one. Instead, to resolve this conflict, the animal would need to use the functionally overlapping problem. Again, regardless of whether the animal could resolve this conflict or not, the animal's performance could be continuously coded as it would interact with the problem. In principle, one could also introduce the overlapping problems in another order: the perceptually overlapping first, and then the functionally overlapping one to compare how the order of presentation influenced the performance in the test. However, as the number of animals involved in such experiments is usually limited, such comparisons have lower priority than the comparison between having the two conflicting trainings and having only a helpful one. Finally, following the Kokinov's priming experiments, one should test, how the animal would perform, if it received just one helpful training. Again, in principle, one could also test how the animal would perform only after a hindering training instead, but this could be as well tested in the future.

These ideas were transformed into an experimental setup for great apes and Goffin's cockatoos within the scope of this thesis. The experiment comprised of three conditions: a control, in which there was no training in between the two exposures to the test problem; a no-conflict condition, in which there was a helpful training before the second exposure to the test problem; and a conflict condition, in which there was a helpful training, followed by a hindering one, before the second exposure to the test problem. To ensure that the animals used long-term memory upon the second exposure, there was always a 24-hour delay between any experiment-related activity and the second exposure to the test. For details of the procedure and the results please see Papers I and II.

Until now, we have discussed what memory is for, which mechanisms could support it and what is known about animal memory. In fact, we focused predominantly on retrieval from *long-term memory*. This retrieval is subject to executive control, relies on cooperation between the prefrontal cortex and the hippocampus, includes different types of information and can be simulated by computer models. However, neither of the models – Kanerva's sparse distributed memory and Kokinov's AMBR – could model how long-term memory operated without the *focus* – a temporary resource responsible for dealing with currently relevant information. On the one hand, in Kanerva's model, *focus* was defined as a part of architecture tasked with meshing and matching between information acquired by the senses and information available in the memory. On the other hand, in Kokinov's model, *focus* was defined as the most active part of architecture, and the most active part of so-called *working memory*, that is a set of agents whose activation exceeded a certain threshold. Both of these definitions point to the same function of the focus: active processing of the ever-changing influx of information to meet the goals of the system on the one hand, and the dynamically changing environmental demands on the other. The capacity for meeting these demands has been repeatedly investigated in the last decades in humans and some animals, under the names of *attention* and *working memory*. Without the processes of attention and working memory, we could never deal with the information obtained in immediate contexts and build up our long-term memory. In other words, many of our long-term memories would never be formed, if it was not for working memory and attention. The answer to the question tackled in this part of the introduction, that is, *what and how animals remember*, would be greatly incomplete without considering how animals acquire and process information in immediate contexts. For this reason, we first need to understand what working memory is, how it is related to long-term memory, and how the prefrontal cortex and the hippocampus are involved in the processing of the immediate contexts, just like they were in the retrieval from long-term memory. Hopefully, before we move on to part 4, we will have a better overview of how various aspects of memory serve the same function: of flexible adaptation to the dynamically changing environment.

Attention

We deal with dynamically changing environments on a daily basis. As we are equipped with complex perceptual systems (Gibson, 1966) that grant access to abundant and detailed information about the continuous changes in the environment, we have access to a multimodal perceptual input: a teeming variety of sights, sounds, smells and sensations (Buchsbaum & d'Esposito, 2008). Because we cannot process all the information available at any given moment, we need mechanisms that will select important pieces of information over other, less important ones. Further, this selected information needs to be processed: cut into processable units (Pöppel, 2004), compared with memory traces (e.g., Kanerva, 1988), and, under certain circumstances, incorporated into long-term memory. These mechanisms – of dealing with the influx of perceptual information – are termed *attention*. Without attention, learning and memory would be significantly crippled, if not impossible.

The attentional mechanisms carry out multiple processes that serve three general functions: basic, selective and executive (Sarter & Demeter, 2008). On the first, basic level, the attentional mechanisms support our *alertness*, that is, general readiness for input processing. We must be alert to pick up and keep up with the influx of perceptual information coming from the environment. Once the information can flow into the system, the attentional mechanisms take on the second, selective function, and select the more important pieces of information over the less important ones. This selection can be guided by either the perceptual or the memory input. Whenever a certain salient or unexpected object in the environment would catch our attention, the object was selected in a *bottom-up* way: something in the perceptual input guided the attentional mechanisms to direct the available resources toward that particular object (Theeuwes & Burger, 1998; Yantis & Hillstrom, 1994; Sarter & Demeter, 2008). Alternatively, we can also use previous practice, knowledge or expectations to come up with a certain object template (Duncan & Humphreys, 1989; Soto, 2005) and seek after this template by sieving the perceptual input. Whenever we use the memory input to search for specific information, we engage in a *top-down* selection. Selecting information – both in the bottom-up and in the top-down way – leaves us with a pool of unsorted information, all of which was important enough to enter the system. To deal with this pool effectively, the attentional mechanisms have to play a third, executive role: they need to sort and prioritise some pieces of information over the other. This prioritisation must be aligned with the limited attentional resources, the current goals of the organism and the ongoing environmental challenges.

Both the selective and the executive functions determine what will survive the immediate moment and enter long-term memory, which, as we have already learned, relies on the hippocampus and the prefrontal cortex. But accumulating information in long-term memory would not be possible if it was not for brainstem and basal forebrain ascending systems. These systems are responsible for the basic function of the attentional mechanisms, as they modulate general readiness of the forebrain (including the hippocampus and the prefrontal cortex) for input processing (Sarter & Demeter, 2008). However, in the recent years, it became clear that these systems are equally crucial for learning and memory-based tasks that require detection, selection and processing of the perceptual information. They modulate which information will be integrated into the processing stream, and so influence the following behavioural response (Sarter & Demeter, 2008). Specifically, the ascending systems include the noradrenergic and the cholinergic system, both of which play a crucial part in the predict-implement-update-predict loop. On the one hand, the noradrenergic system is responsible for selective responding to stimuli and a shift in alertness whenever new events or unexpected behavioural outcomes occur (Aston-Jones, Chiang, & Alexinsky, 1991; Foote, Berridge, Adams, & Pineda, 1991; Usher, Cohen, Servan-Schreiber, Rajkowski, & Aston-Jones, 1999). To serve these two functions, it can encode the outcome of behavioural responses, and support adjusting the performance to the ever-changing external challenges (Clayton, Rajkowski, Cohen, & Aston-Jones, 2004). On the other hand, the cholinergic system facilitates the executive control exerted by the prefrontal cortex, as it supports detection of cues, disengagement from ongoing activities and orientation toward the source of the cues (Sarter & Demeter, 2008). Removing the cholinergic inputs to the prefrontal cortex results in a persistent and profound disruption of several attentional mechanisms (Voytko et al., 1994; Chiba, Bucci, Holland, & Gallagher, 1995; McGaughy, Everitt, Robbins, & Sarter, 2000; Turchi & Sarter 1997, 2000; Burk & Sarter 2001; Burk, Herzog, Porter, & Sarter, 2002; Berntson, Shafi, Knox, & Sarter, 2003; Dalley et al., 2004; Martinez & Sarter, 2004), such as sustenance of attention (McGaughy, Kaiser, & Sarter, 1996) and detection of cued stimuli (Chiba, Bushnell, Oshiro, & Gallagher, 1999), showing that the cholinergic inputs are crucial for accurate prefrontal processing.

Top-down selection of information in the perceptual input relies on memory: previous practice, knowledge and experience. In sparse distributed memory model, the information retrieved from memory met the information received within the perceptual input in a part of the architecture called *focus*. This definition was quite narrow: it was constrained to the top-down selection, as the focus comprised of potential cues from the perceptual input and traces from the memory input. On the other hand, in the AMBR model, *focus* was defined as the most active set of all agents that exceeded a certain activation threshold and entered *working memory.* The term of *focus of attention* has also been repeatedly used in psychological literature, but there is no consensus as to what this term means. Its definition can be similar to Kokinov's; for instance, Nahid Zokaei and colleagues defined it as a "more prioritised state" of some pieces of information, out of all the information currently available to the attentional mechanisms (Zokaei, Ning, Manohar, Feredoes, & Husain, 2015). According to this definition, the information can be brought to the focus of attention both in the above-mentioned bottom-up and top-down ways. However, others, such as Nelson Cowan and Klaus Oberauer, defined the focus in another way (Cowan, 1995, 1999; Oberauer, 2002). According to the AMBR model, neither the focus nor long-term memory was limited. However, according to Cowan's and Oberauer's approach, whereas the activated part of long-term memory is not capacity-limited, the focus of attention has a limited capacity (Cowan, 1995, 1999; Oberauer, 2002). Regardless of this difference, both this approach and the AMBR model agree that both the (sufficiently) activated part of the long-term memory and the focus of attention constitute *working memory*.

The interplay between attentional mechanisms and working memory has again been explained in different ways in psychological research (Zokaei et al., 2015). These explanations, in general, come from one of two approaches: in the first, developed by Cowan (1988, 1995, 1999) and Oberauer (2002, Oberauer et al., 2009), working memory emerges from selective attentional mechanisms directed toward information stored in long-term memory; in the second, initiated by Alan Baddeley and Graham Hitch in 1974, the attentional mechanisms relate to a central executive that controls and supervises several working memory resources (Baddeley & Hitch, 1974; Baddeley, 2000; Abrahamse, Majerus, Fias, & van Dijck, 2015). To understand how the concepts of attention, working memory and long-term memory relate to one another, we first need to have a closer look at how the concepts of working and short-term memory evolved over the years.

Working memory

The terms of working and short-term memory emerged in the 1950s, and have both gone a long way since then. Initially, they described a passive store-like memory resource: a place in or a part of the memory system, in which information was temporarily stored for immediate use (Newell & Simon, 1956; Miller, Galanter, & Pribram., 1960). Then, in the 1970s, the emphasis shifted for the first time: working memory was no longer merely a passive store, but a combination of storage and processing (Daneman & Carpenter, 1980). And after the 1980s, the emphasis shifted again, toward a more processual approach, as working memory became more and more tied to executive functioning (Cowan, 1988; Engle, 2002).

That memory is not a uniform construct, and comprises of at least two distinct systems, became clear in 1957, when William B. Scoville and Brenda Milner (1957) described a case of H. M.'s memory. H. M. was a 29-year-old motor specialist who suffered from epileptic seizures since he was 10, after being knocked down by a bicycle at the age of 9. As he did not respond to maximum doses of conventional medication, he underwent a so-called bilateral medial temporal-lobe resection. In practice, this meant that he lost large parts of the hippocampus, and, as a result, the ability to permanently store new pieces of information, such as facts and events. H. M.'s long-term memory was profoundly disturbed; but his short-term memory seemed intact, as he was still able to temporarily store and repeat back, for instance, a series of digits (Buchsbaum & D'Esposito, 2008). This distinction between temporary and permanent storage in the behavioural outcome spurred a distinction between short-term memory, responsible for temporary maintenance, and long-term memory, responsible for permanent maintenance of information.

The term of *short-term store* was first used by Donald Broadbent in 1958, followed by George Sperling's *short-term memory* in 1960. They used this term to describe a decaying sensory trace (Cowan, 2017), which today would be described as *sensory memory*. The *short-term store* gained a new meaning in 1968, when Richard Atkinson and Richard Shiffrin put forward their influential multistore model of memory (1968). According to their model, the short-term store received selected information from the sensory registers (perceptual input) and from long-term memory store (memory input). In other words, the short-term store was a passive middleman between the sensory registers and long-term memory, and, to reach the long-term memory store, the newly acquired pieces of information had to pass through this middleman. In this model, only the sensory registers were specialized in dealing with a specific sort of input, for instance, visual, or auditory, or haptic (*domain-specific)*. These different sorts of inputs ended up in the short-term store, which was not specialized (*domain-general*) in the model; although the authors did not exclude the possibility that the short-term store likewise comprised of more specialized sub-stores, they decided that there was no sufficient empirical evidence at that time to support the existence of such sub-systems and their inclusion in the model. Such subsystems were introduced six years later, in 1974, when the short-term store became a part of working memory (Baddeley & Hitch, 1974).

The very term of *working memory* was introduced in the 1950s, and was first used in relation to computer memory. Namely, in 1956, Allen Newell and Herbert A. Simon wrote about a computer *working memory*, which was basically a place that temporarily stored information for immediate use (Newell & Simon, 1956; Cowan, 2017). The term was soon adopted by psychologists, and in 1960 Miller and colleagues used the term of *working memory* to describe a part of the mind that stored information about goals that were prerequisite for carrying out actions in the environment (1960). Then, fourteen years later, *working memory* met *short-term store* in a multicomponent model put forward by Alan D. Baddeley and Graham Hitch (1974). The multicomponent model evolved from the multistore model introduced by Atkinson and Shiffrin (1968). It was no longer a storage-based system; now it included passive stores that held currently available information for active processing that would extend longevity of the held information. The short-term store itself was no longer unitary; now it comprised of two specialized stores: a phonological and a visuospatial one (Baddeley, 1986). In this model, the sensory information was first analysed in perceptual modules (earlier: sensory registers), and then transferred into specialized stores that temporarily held this information (earlier: a domain-general store). These stores would hold information for a certain limited time regardless of the processes that could extend such maintenance. Each of these passive stores was accompanied by an active process that perpetuated the held information and prevented its decay (Cowan, 2017). The first process, so-called articulatory rehearsal, operated on the information in the phonological store; together they formed the *phonological loop* that stored and maintained information in a verbal form. The second process, so-called saccadic rehearsal, operated on the information stored in a passive visual store, with which it formed the *visuospatial sketchpad* that stored and maintained visuospatial information. Senses other than vision and – to some extent – hearing - were not introduced the model. With only two systems – the phonological loop and the visuospatial sketchpad - the multicomponent model accounted only for the perceptual input into working memory, and not for the input from long-term memory. It changed in 2000, when Baddeley, alongside the two already-mentioned systems, introduced a third one: a so-called *episodic buffer*. This additional system could store and maintain associations between different kinds of information and opened the model up for the input from long-term memory. In all versions of the model, the operation of the sub-systems – the phonological loop, the visuospatial sketchpad, and later the episodic buffer – was controlled and supervised by a so-called *central executive* that managed the flow of information in and out of the sub-systems.

The idea of passive store-like character of working memory did not hold for long. In yet another approach to working memory, Cowan put forward a more generic definition (Cowan, 1988; 2017), according to which, working memory was composed of any information temporarily held in any form. As it was unclear which and how many working memory modules existed, there was no point in speculations about the number and the character of the hypothesized stores. To avoid such speculations, working memory became solely an information-processing system. The perceptual input entered a stream of information processing through a brief sensory store and joined the activated information from long-term memory. Together, these pieces of information – from the senses and from long-term memory – formed a pool of currently available information. Within this pool, executive processing could bring different pieces of information to the focus of attention. Because this focus of attention had a limited capacity and could process roughly three to four items, only some of the currently available information could be simultaneously analyzed (Cowan, 1988; 2017).

The role of central executive was prominent in both Baddeley's and Cowan's models, but only Randall W. Engle equaled the concept of working memory to so-called executive attention, blurring the line between the two (2002). In his definition, working memory was described as the use of attention to manage goals and select some over the other. Executive attention operated in conjunction with short-term storage mechanisms that held relevant information, but did not require attentional processing. In this model, the specialized stores were back in place to hold information, which was efficiently used by the executive attention processes. However, Engle and colleagues (e.g., Engle 2002; Engle & Kane, 2004; Kane & Engle, 2002; McVay & Kane, 2009) were no longer interested in the short-term storage processes, as they were no longer a part of working memory. Working memory was now solely about attention-control processes, that is, the operation of the central executive in the previous models. Further, Engle suggested that working memory capacity, or executive attention, was particularly important in situations that required a resolution of conflicting response tendencies, retrieved from long-term memory (2002). Therefore, working memory capacity was crucial for issuing a flexible behavioural response to a problematic situation that partially overlapped with some previous situations that led to contradictory behavioural responses. In other words, working memory capacity was crucial for dealing with the conflict at hand, even if the conflict was spurred by the records retrieved from long-term memory. Before we further explore the links between working and long-term memory – let us have a closer look at the issue of capacity and capacity limits within working memory.

Capacity limits

We have already learned that the focus of attention has, at least according to some, a limited capacity of three to four items (Cowan, 2001). However, whether such capacity limits exist, and how large they are, is a much-debated issue. According to Cowan, already in 2001, there were at least seven different answers. Those that contested the existence of such limits, contested the very existence of short-term memory (Crowder, 1982; Cowan, 2001). And those that accepted the existence of the latter, in general agreed that some capacity limits were in place. Some of the short-term memory proponents argued that different types of material (Wickens, 1984) and different tasks (cf. task-specific account, Cowan, 2001) had different material-specific or task-specific limits; others offered different capacity limits for storage and processing (Daneman & Carpenter, 1980; Halford, Wilson, & Philips, 1998). And finally, the last group, including George A. Miller (1956) and Nelson Cowan (2001) favoured fixed capacity limits. They both also proposed that this fixed limit can be overridden by a cognitive strategy, called chunking. Chunking allows for cutting a series of information into smaller portions, for instance, when we group a long phone number into two- and three-digit chunks. The digits that end up in one chunk will be more related to each other, for instance, follow each other in closer temporal and spatial proximity, than to the digits that belong to other chunks. Chunking strategies can be applied to different sorts of information. For instance, Miller suggested that a sequence of inputs can be recorded under a concise name, turning it into a single input freeing up space for other inputs. Because assigning the name to the sequence of inputs relied on records associated with this name in long-term memory, the contents of long-term memory could influence the contents of working memory. According to this approach, working memory could hold from 5 to 9 chunks at any given moment.

Cowan (2001) supported a smaller capacity limit – of 3 to 5 chunks – but, as we have already learned, agreed that the contents of long-term memory influenced the contents of working memory. After all, working memory consisted, to a great extent, of an activated portion of long-term memory. According to Cowan's approach, this activated portion of long-term memory was not limited by capacity, but by time and susceptibility to interference between concurrently activated items. The capacity limit was only imposed on the focus of attention, in which it could be, like in Miller's approach, overridden by chunking. Although the number of chunks was limited to a maximum of 5 chunks, the amount of information available in these chunks could, in principle, remain unlimited (Cowan, 2001). The size of chunks was, for instance, dependent upon long-term memory, as Gobet and Simon (1996, 1998) showed in expert and non-expert chess players. While the number of chunks was the same for all players, the degree of expertise correlated with the size of the chunks; namely, the expert players could hold more information within each chunk than the non-expert ones. Recently, Thalmann, Souza, and Oberauer (2018) confirmed this finding experimentally, as they showed that chunking could indeed reduce the load on working memory and rely on long-term memory. The authors suggested the following relation between these two memories. When individual items are encoded into working memory, they may be compared with records of previous chunks detected in long-term memory; if a matching record is found, it is retrieved and encoded into working memory.

Let us imagine that the individual items are like eggs that are being put into an egg shelf in the fridge. Some of these shelves have an egg rack, that is, a piece of wood, plastic or metal with cut-out holes, which can securely hold a bunch of eggs. Using the egg rack – a chunking template retrieved from long-term memory – allows for putting together a number of eggs which would otherwise fill up the whole shelf, changing position with each opening of the fridge. The relevant templates retrieved from long-term memory are encoded into working memory, just like the egg-rack is inserted into the fridge shelf. The templates put the items together and, in a sense, create an egg-rack with six eggs instead of six single eggs, freeing up space for inserting the next ones.

However, it seems that these chunking templates may apply rather to complex real-world objects than to simple stimuli, such as colours or orientations (Brady, Stormer, & Alvarez, 2016). Because such templates for simple stimuli are not available in long-term memory, the capacity limit for simple stimuli may be filled up more rapidly than for the real-world objects. For instance, Brady and colleagues found that when participants had more and more time for acquiring information about the simple stimuli on one hand and the real-world objects on the other, they showed a small capacity limit for the simple stimuli, and virtually no limit for the real-world objects. As the participants were given more and more time, they were able to acquire and store more and more detailed information about the real-world objects. This was not the case for the simple stimuli: already within the first 100 milliseconds of the encoding time, the participants' working memory filled up, and the capacity limit was reached. Therefore, Brady and colleagues (2016) showed that the relevance of the presented stimuli played a role in encoding into working memory, just like it plays a role in encoding, storage and retrieval from long-term memory (Konkle, Brady, Alvarez, & Oliva, 2010; McWeeny, Young, Hay, & Ellis, 1987; Bower, Karlin, & Dueck, 1995). In a similar vein, the capacity limit for complex-but-meaningless objects may be even lower than the limit for the simple stimuli (Luria, Sessa, Gotler, Jolicoeur, & Dell'Acqua, 2010).

It seems the participants could actively operate on a greater amount of information in working memory when they dealt with meaningful and relevant objects. But meaningfulness might not be the only aspect that supports such encoding. In fact, cross-modal objects, that is those that engage more than one sense, e. g., vision and hearing, are remembered better than modality-specific objects (Thompson & Paivio, 1994; Goolkasian & Foos, 2005; Delogu, Raffone, & Belardinelli, 2009), and, likewise, working memory capacity for such cross-modal objects can be greater than for unimodal ones (Saults & Cowan, 2007; Fougnie & Marois, 2011). Therefore, both robust cross-modal information and meaningfulness may contribute to complex high-resolution bindings, which are supported by the hippocampus (Yonelinas, 2013). The role of the hippocampus in working memory is not as straightforward as it was in long-term memory. Nevertheless, a damage to the hippocampus can disrupt performance on some working memory tasks, which suggests that it must be somehow responsible for the related information processing. As we might remember, the hippocampal damage did not affect H.M.'s short-term memory, and in fact, it seems that working memory for digits and other single items, such as words or locations, could remain unaffected by such damages. However, real-world objects and events do not comprise of single features or simple associations; they are multimodal and require remembering multiple features and complex associations between these features. For instance, on a daily basis, we need to remember precisely where objects were when we last saw them, or how different objects or people were located with respect to one another. When we recall what exactly happened between two people in the street, one of whom is now covered in blood, we need to report precise information about what, where and how happened, who was involved, and which objects were used to cause the resulting effect. This ability – of binding all these features of a certain past situation – relies on the hippocampus. But to remember this binding after a delay, we need to encode it in working memory first, and it seems that the ability of such complex and high-resolution binding within working memory is impaired after hippocampal damages (Jeneson, Mauldin, & Squire, 2010; Watson, Voss, Warren, Tranel, & Cohen, 2013; Warren, Duff, Tranel, & Cohen, 2010; Hannula, Tranel, & Cohen, 2006; Quak, London, & Talsma, 2015).

Working versus long-term memory

There is no consensus as to what working memory is, and whether it is limited or not. Likewise, there is no consensus on the relationship between working memory and long-term memory. The views on this relationship range from complete independence (e.g., Baddeley, 1986; Barrouillet & Camos, 2015), through partial dependence (e.g., Cowan 1999; Oberauer, 2002), to no distinction between working memory and long-term memory whatsoever (Crowder, 1982; Nairne, 2002). According to the view of complete independence, working memory and long-term memory serve two non-overlapping functions, and therefore represent two functionally distinct aspects of memory (Unsworth, 2010). Specifically, working memory is responsible for storing and manipulating a small portion of information relevant in the immediate context; conversely, long-term memory is responsible for storing all previously acquired records of the past. Because of this functional difference, the information stored in each of these two systems is prone to different mechanisms of transformation and loss: decay over time in working memory, and interference in long-term memory (Unsworth, 2010). This view was, for instance, shared by Baddeley (1986, 2007) as well as Schacter and Tulving (1994). According to another extreme view, in which there is no distinction between working and long-term memory, dealing with immediate and delayed contexts relies on a single unitary memory system (Crowder, 1982; Melton,1963; Nairne, 2002; Surprenant & Neath, 2008).

However, based on the above-mentioned findings, it seems that the lack of distinction between working and long-term memory is not consistent with H.M.'s selective disruption: a complete loss of long-term memory and a retention of more-or-less intact working memory skills (perhaps with a limited access to high-resolution binding). Complete independence between working and long-term memory also does not seem to hold, as records stored in long-term memory can influence the size of chunks and facilitate processing of real-world objects over simple stimuli. Therefore, the intermediate view, in which working memory comprises of sensory information and the activated content of long-term memory (Cowan, 1999; Oberauer, 2002), seems to fit best with the above-mentioned findings. According to this view, there is a partial overlap between working memory and long-term memory, and, therefore, they are used conjointly in everyday situations. However, as they do not overlap fully with each other, the overlap in neural networks that support working vs. long-term memory should only be partial, and, likewise, working and long-term memory should have both overlapping and unique properties.

Working and long-term memory should be related, but somewhat distinct (Unsworth, 2010). In accordance with this approach, the relationship between working and long-term memory seems to be bidirectional (Loaiza & Camos 2018;

Loaiza & Halse, 2018). Working memory influences episodic long-term memory (Camos & Portrat, 2015; Loaiza & McCabe, 2012, 2013; McCabe, 2008), and long-term memory in turn influences working memory (Loaiza & Camos, 2018; Loaiza, McCabe, Youngblood, Rose, & Myerson, 2011; Rose, Buchsbaum, & Craik, 2014). First, increasing the number of distractors in a working memory task facilitates better retrieval of this task from episodic long-term memory after a delay (Loaiza & Halse, 2018). Second, when participants encode a list of consecutive items while solving non-related problems, they also remember those items better after a delay, than when they encode the list without such concurrent problem-solving. This relationship is called *McCabe effect*. Third, a similar effect was also detected in another task, in which participants encoded twice-presented target items. Some target items were presented twice with an unfilled interval in between, and for the remaining target items some distracting items were presented in the interval. Interestingly, right after the presentation, participants remembered the two targets that were not separated by the distractors better than those that were separated by the distractors. However, after half an hour, the participants showed better recall for the items separated by the distractors. All in all, putting an additional load on working memory, and forcing the immediate processing to resolve interference between competing items, improves delayed recall. In other words, dealing with an immediate conflict in working memory supports later retrieval from long-term memory.

Back to the central executive

In part 2, we learned that the prefrontal cortex was responsible for resolving conflicts between the newly acquired experiences and the records retrieved from long-term memory, and, in general, worked as the ultimate conflict resolver in our brain. Therefore, we might expect that resolving conflicts in immediate contexts likewise engages the prefrontal cortex. This intuition is correct, as this brain area is crucial for prioritising and selective allocation of attentional resources to currently relevant goals (Rossi, Pessoa, Desimone, & Ungerleider, 2009). In fact, the concept of working memory as executive attention, introduced by Engle in 2002, may, to a large extent, overlap with the concept of executive functioning (2002), which was likewise described in part 2.

The prefrontal cortex oversees the executive control, a top-down influence on a range of psychological processes (Shallice & Burgess, 1996; Smith & Jonides, 1999; Miller & Cohen, 2001). The mechanism that supports such executive control received two different names in experimental psychology and neuropsychology. Experimental psychologists assigned the executive control to *working memory capacity* (Baddeley, 1986), and investigated the role of working memory capacity in controlling attention under conditions of interference and distraction (Engle & Kane, 2004). Conversely, neuropsychologists assigned the executive control to *frontal-lobe*, or *executive*, *functioning* (Carlson, 2005; Fuster, 1997; McCabe, Roediger, McDaniel, Balota, & Hambrick, 2010; Salthouse, Atkinson, & Berish, 2003; Stuss & Knight, 2002), and investigated the relationship between the frontal-lobe functioning and the control of goal-directed behaviour, especially under novel circumstances (Banich, 2009; Lezak, 1995; Fuster, 1997).

Despite this terminological difference, both concepts – of working memory capacity and frontal-lobe functioning – put emphasis on the same function: control of attention directed at conflict resolution. Moreover, both working memory capacity and frontal-lobe functioning were central to theories of episodic memory, and both were strongly related to episodic memory performance (McCabe et al., 2010). Specifically, both working memory capacity and executive functioning predict performance on several attention-demanding episodic memory tasks (Oberauer, 2005; McCabe et al., 2010), and both mediate age-related differences in episodic memory (Park et al., 1996; 2002; Bugaiska et al., 2007; Ferrer-Caja Crawford, & Bryan, 2002; McCabe, Roediger, McDaniel, & Balota, 2009; Taconnat, Clarys, Vanneste, Bouazzaoui, & Isingrini, 2007; Troyer, Graves, & Cullum, 1994). Based on these findings, David P. McCabe and colleagues suggested that these concepts may also share a common underlying attentional ability (2010) called *executive attention* after Engle and colleagues (Engle & Kane, 2004; Kane & Engle, 2002; McVay & Kane, 2009). After comparing performance on several working memory capacity, executive functioning and episodic memory tasks in 18- to 90-year-old participants, they found that the tasks that supposedly tapped into working memory capacity and executive functioning, in fact measured a very similar construct of the executive attention. They hypothesized that executive attention had two main responsibilities: maintaining a goal throughout the task and resolving interference, particularly when a prepotent behavioural response and task demands were in conflict. They also showed that age-related decline in episodic memory was driven by age-related declines in working memory and executive functioning, confirming that both constructs were profoundly related to episodic memory.

Age-related decline in performance on working memory and executive functioning tasks has also been found in some animal species, such as rats and pigeons (Bizon, Foster, Alexander, & Glisky, 2012; Coppola, Hough, & Bingman, 2014). This decline has been tied to changes in the prefrontal cortex and the hippocampus in rats (Bizon et al., 2012), and the functional analogue of the hippocampus in pigeons, the hippocampal formation (Coppola et al., 2014). The pigeon's functional analogue of the prefrontal cortex, called nidopallium caudolaterale, has not been tied to this age decline yet; however, as the nidopallium caudolaterale was linked to working memory in carrion crows (Veit, Hartmann, & Nieder, 2014; Hartmann, Veit, & Nieder, 2018) and executive control in pigeons (e.g., Rose & Colombo, 2005), it is only reasonable to suspect that this area may also be involved in age-related decline of performance on the corresponding tasks.

Comparative studies of the interplay of working memory, executive functioning and long-term memory can reveal cross-species similarities and differences as to how animals and humans use their memory. But such comparative studies can also serve another purpose – of investigating which aspects of working memory, and so memory in general, may be available to all animals with the prefrontal cortex or the nidopallium caudolaterale, and which may be available uniquely to humans. Speculating about the uniquely human aspects of cognition does not belong to the scope of this introduction because, on one hand, too little is still known about animal memory, and on the other, recent findings point to more similarities than differences in some memory processes in animals and humans (Roberts & Santi, 2017). Taking the lack of evidence for the evidence of the lack could only lead to unsubstantiated claims about differences between animal and human memory and could potentially hinder the investigation of similarities between the two. Before we proceed to exploring possible similarities between animal and human working memory, let us find out how one can test working memory without words.

Working memory in animals

Although the term of working-memory was first used only in the 1950s, the interest in animal memory for immediate contexts dates back at least to 1913 and Walter S. Hunter's *delayed-response* task (Dewsbury, 2000; Hunter, 1913; Roberts & Santi, 2017). In this task, an animal was typically constrained to a compartment with an outlook at three nearby doors. Above each door, there was a switched-off light, one of which would switch on in full view of the animal at a certain point during the experiment. The light above one of the doors signalled that behind this door and this door only, a reward was waiting for the animal. The light soon would switch off, and after a certain delay, the animal would be released from the compartment and could choose one of the doors. Obviously, the choice was correct only if the animal chose the baited door. Hunter (1913) tested three animal species in this setup: a rat, a raccoon and a dog, finding that each of the species started to make mistakes after a varying delay. This delay, called *retention interval*, equalled 10 seconds for rats, 25 seconds for raccoons and impressive 5 minutes for dogs. The differences in the retention interval played well into contemporary efforts of establishing a hierarchy of animals, with those that could wait longest at the top, and those that would fail after shortest intervals at the bottom. However, establishing such a hierarchy proved difficult, if not impossible, as the performance was found to depend more on setups and experimental procedures than on the choice of species (Roberts, 1998). For instance, in Hunter's study from 1913, the dogs simply oriented the body toward the correct door when the light was switched on and remained in this position for several minutes, contrary to the rats and the raccoons that did not orient the body toward the signal. Once the dogs were released from the compartment, they headed in the direction that overlapped with their body orientation.

Before the 1950s, the delayed-response task, in various versions, was tested with a range of animals, such as primates, from lemurs to orangutans and chimpanzees (Harlow, 1932; Harlow, Uehling, & Maslow, 1932; Maslow & Harlow, 1932; Yudin & Harlow, 1933; Tinklepaugh, 1932), New World monkeys (Harlow & Bromer, 1939), and rats (McAllister, 1932). This task was not only used to test memory skills in healthy animals; it was also adopted by Carlyle F. Jacobsen to study memory impairments in chimpanzees with lesions of the prefrontal cortex (1936). He used a version of another task introduced by Hunter (1913), in which an animal observed hiding of a food reward in a certain location and could search for it after a certain delay. The item was hidden in one of the wells (Hunter, 1913) or boxes (Jacobsen, 1936) in a full view of the animal, but to later find the hidden food reward, the animal had to operate on items that were no longer available in the visual field. Specifically, while the reward was still visible at the beginning of the trial, the animal had to encode the item and the location in which it was subsequently hidden; once the item was no longer visible, the animal had to hold it "online" in working memory; and once the opportunity of getting the item appeared, the animal should have engaged in a motor action: seek after the reward in the correct location (Buchsbaum & D'Esposito, 2008). The healthy chimpanzees could carry out all of these three steps; but those that suffered a lesion to the prefrontal cortex, were not capable of fulfilling the second step and therefore failed the task (Jacobsen, 1936).

The delayed-response task belongs to a larger family of delay tasks, in which a retention interval is administered between the exposure to certain stimuli and the opportunity of behavioural response on the animal's part. All tasks in this family require the same general three steps – encoding, "online" maintenance, and issuing a behavioural response; however, some rely on encoding and maintenance of spatial information, and others require operating on non-spatial information instead. The spatial (navigation) tasks include the already-described *delayed-response* task and the *delayed-alternation* task; the non-spatial tasks may require *delayed-matching-to-sample* or *delayed-non-matching-to-sample* tasks (Funahashi, 2017).

The *delayed-alternation* task was first used in rats by Harvey Carr in the early 1900s (1917, 1919), and was later picked up in the 1930s in tests of rats (Loucks, 1931), raccoons (Elder & Nissen, 1933), and chimpanzees (Nissen & Taylor, 1939). In a typical delayed-alternation task, an animal needs to navigate in a maze consisting of at least three arms. The maze can be T- or Y-shaped, or radial. Regardless of the maze's shape, the animal should enter the arms, one after another, to retrieve food items from the farthest ends of these arms. In T-shaped and Y-shaped mazes, the animal typically starts the task from the longest arm and can choose either of the two shorter ones; conversely, in the radial mazes (first in Olton

& Samuelson, 1976; Zoladek & Roberts, 1978), the animal usually starts from a central hub and then proceeds to the eight arms that radiate outward and so create an asterisk-like shape with the hub in the center. In the delayed-alternation task, the animal should typically explore the available arms, one after another, without coming back to any already-explored arms. This task has become increasingly popular since the 1970s and Atkinson and Shiffrin's model of short- and long-term storage (1968; Honig & James, 1971).

The radial maze became perhaps the most popular setup in spatial memory studies after the 1970s, as another task from the same family, called *delayed matching-to-*sample, prevailed in non-spatial setups. Although the delayed-matching-to-sample was initially designed for chimpanzees in the 1940s (Finch, 1942), it has since been tested in a range of animals, such as mice (e.g., Yhnell, Dunnett, & Brooks, 2016), rats (e.g., Wallace, Steinert, Scobie, & Spear, 1980; Winters, Matheson, McGregor, & Brown, 2000), pigeons (Roberts, 1980; Roberts & Grant, 1976; Zentall, Hogan, & Moore, 1978), jungle crows (Goto & Watanabe, 2009), scrub jays (Olson, Kamil, Balda, & Nims, 1995), rhesus macaques (e.g., Davachi & Goldman-Rakic, 2001; Lee, Conroy, McGreevy, & Barraclough, 2004; Scott, Mishkin, & Yin, 2012), chimpanzees (e.g., Finch, 1942; Beran & Washburn, 2002), gorillas (Vonk, 2003), orangutans (Vonk, 2003) and other. In a typical *delayed matching-to-sample task*, an animal is first presented with a certain to-be-remembered item. After this presentation and a given retention interval, the animal is exposed to a set of at least two items, including the already seen one. Now, in the *matching-to-sample* task, the animal, upon this second exposure, needs to choose the to-be-remembered item from among the distractors to obtain a reward. Conversely, in another variant of this task, so-called *non-matching-to-sample*, the animal should now choose an item that is different from the to-be-remembered one.

Using such delay tasks allows for investigating whether animal and human working memory are enhanced or hindered in similar experimental procedures. If similar procedures triggered similar improvements or impairments of performance in mammals, birds and humans, one could infer that mammalian, avian and human working memory could rely on similar mechanisms. It seems that there are several parallels between mammalian, avian and human working memory, as numerous studies showed in recent years (Roberts & Santi, 2017). These studies usually introduced diverse versions of delayed matching-to-sample setups to induce either enhancing or hindering effects on working memory of the tested species. Some animals, like humans, improved on working memory tasks after practice. For instance, pigeons trained on fixed delays in a delayed matching-to-sample task could retain the sample and make a correct choice in the test after longer and longer delays (Grant, 1976). This effect – of extending the retention interval after training – suggested that information loss in the pigeons' working memory did not simply result from decay in a passive short-term store, but was subject to active processing that likely became more and more efficient over time. Two other findings from pigeon studies showed that the animals indeed actively processed the acquired information. Pigeons, like humans (Tulving et al., 1996; Habib et al., 2013), showed better memory for surprising or novel samples than for expected ones (Maki, 1979), and, further, this advantageous effect of surprise and/or novelty was more pronounced after a delay than in the immediate context (Grant, 1983). Specifically, pigeons were more accurate in delayed matching-to-sample when the samples were surprising than otherwise (Maki, 1979), and this effect of surprise and/or novelty was stronger after 5 and 10 seconds, than immediately after encoding the sample.

However, some animals share the human susceptibility to not only memory-enhancing, but also memory-hindering procedures. For instance, both pigeons (Grant and Roberts, 1976; Roberts and Grant, 1978) and capuchin monkeys (D'Amato, 1973) can suffer a hindering interference effect and suffer a higher forgetting rate, when light is turned on in a dim experimental space at the end of the retention interval, soon before the matching-to-sample test. Interestingly, if the light was turned on at the beginning of the interval, that is right after encoding of the sample, the animals could recover from the interference effect (White & Brown, 2011). When the light was turned on, the animals perhaps acquired new visual information that interfered with the sample maintained in visual working memory. If this interference occurred at the end of the retention interval, the animal had too little time to resolve the interference and recover from forgetting; conversely, when such interference occurred at the beginning of the delay, the animal had much more time to resolve the interference and recover. A similar interference effect was found in rats, although inducing this effect in rats' spatial working memory proved to be much more difficult (Roberts 1981; Roberts & Santi, 2017) than interfering with visual working memory of the pigeons and the capuchins. Neither turning on the light, nor introducing the rats into another similar maze in the retention interval interfered with the rats' memory; these procedures perhaps did not compete for the same working memory resource that was involved in the encoding of the original information. The light could have been encoded as a change in the hue of the environment, and the new maze could have been encoded as a separate "cognitive map" that did not overlap with the map constructed during the initial encoding (Tolman, 1948). Only something that disrupted this original map, could induce the interference effect. When the rat encoded the map, it started from the central hub of the radial maze and always entered the arms through the inner end that was directly attached to the hub. Then it ran to the outer end of the arm, returned to the central hub, entered another arm and so on. To disrupt the map constructed in this way, in the retention interval, William A. Roberts (1981) temporarily introduced the rats to the outer ends of some arms and allowed them to eat up food rewards found in those locations. When the rats entered the maze again after the retention interval, the rats avoided the arms which still contained a reward, but had already been visited within the other procedure in the retention interval.

Some working memory tasks involve encoding of a list of samples instead of a single sample. When human participants later judge which samples belonged to the list and which did not, they usually remember some of the samples better than others. A better recall of some samples depends on the order in which they were presented. Specifically, the participants often remember the first and the last samples better than the middle ones, exhibiting so-called *primacy* and *recency* effects. These effects have been so far established, among others, in chimpanzees (Buchanan, Gill, & Braggio, 1981), rhesus macaques (e.g., Basile & Hampton, 2010; Wright, Santiago, Sands, & Cook, 1985), capuchin monkeys (Wright, 1999); dogs (Craig et al., 2012), rats (e.g., Harper, MacLean, & Darlymple-Alford, 1993; Williams, McKoy, & Kuczaj, 2000), black-capped chickadees (Crystal & Shettleworth, 1994) and pigeons (Santiago & Wright, 1984, Wright et al., 1985). Interestingly, in one of these studies, Anthony A. Wright and colleagues compared rhesus macaques', pigeons' and humans' performance in the same setup, and found both primacy and recency effects in all three species (Wright 1985, 2007, 2013). Right after the encoding, the recency effect was stronger than the primacy effect, but as time went by, the recency effect got weaker and weaker, contrary to the primacy effect that got stronger over time. In other words, right after the encoding of the list, the participants remembered the last seen items best; but after a delay, they started to forget the last seen items, and remembered the beginning of the list better instead. This relationship was found in all three species, but the moment in time, at which the first items began to prevail over the last ones, differed between the species: it was shortest in the pigeons and had only 10 seconds, a bit longer in the rhesus macaques – of 30 seconds, and the longest in humans – of 100 seconds (Wright et al., 1985). Although the retention time for specific items differed between the species, it seems that the primacy and the recency effects are a ubiquitous aspect of both human and animal working memory. This, in turn, suggests that these effects may come from a similar underlying mechanism in both animals and humans.

The serial-position effects, that is the primacy and the recency effects, were initially considered to come from a rehearsal of the encoded items in the short-term storage (Atkinson & Shiffrin, 1968). Atkinson and Shiffrin (1968) suggested that the participants may have more time for rehearsal of the first items on the list than the middle ones, and therefore the first items are more frequently transferred to long-term storage, saved from the decay in the short-term one. On the other hand, the last seen items had the least time for such rehearsal, but, as they have just entered the short-term storage, they were simply most available right after encoding. While this rehearsal theory could hold for humans, it could not explain Wright and colleagues' findings, as the pigeons and the rhesus macaques were considered unlikely to be capable of such rehearsal (Tulving, 2008). Therefore, two other theories seemed to explain these results in a more parsimonious way, in line with above-mentioned Morgan's canon. The first alternative, a so-called discriminability theory, held that the serial position effects arose because the items at the beginning and at the end of the list were more distinctive than those in the middle, and therefore were remembered better than the others (Johnson, 1991; McGeoch, 1942; Murdock, 1960; Ribback & Underwood, 1950). However, the discriminability theory alone failed to account for the shift from recency to primacy as the delay increased (Tulving, 2008). This issue was addressed by Tulving (2008) who suggested that there was no reason to treat the primacy and the recency effects as two sides of the same coin, as they did not need to rely on the same mechanism. In fact, the primacy and the recency effect are affected in different ways by certain experimental procedures, e.g., by the level of alcohol in blood (Jones, 1973; Tulving, 2008). If these two effects – of primacy and recency – rely on two separate mechanisms, it is possible that right after encoding, the primacy effect is present but simply overshadowed by the recency effect; and as the recency effect wears off, the primacy effect becomes more and more pronounced. According to Tulving's hypothesis, the primacy effect does not appear after a given interval – of 10, 30 or 100 seconds, but only resurfaces from underneath the recency effect. The primacy effect emerges in both animal and human memory because it depends on the activity of neural networks that are responsible for encoding the list. Once the first sample is encoded, the network uses up a certain amount of energy and suffers fatigue. If the second sample on the list requires the activity of the same neural network, the network cannot deal with it as efficiently as with encoding the first sample; therefore, the recall for this and all other subsequent samples is worse than for the first sample on the list. The same mechanism could underlie the already-mentioned surprise/novelty effect (Kormi-Nouri, Nilsson, & Ohta, 2005), resulting in a better memory for the first surprising and/or novel item than the following ones.

It seems that animal and human performance in at least some working memory tasks relies on the same principles: it can improve or decline under similar circumstances, and so it perhaps relies on similar mechanisms. Animals, just like humans, seem to process and lose information in various ways, and are not constrained to passive storage and decay. If this is indeed the case, animal working memory should also require neurocognitive machinery that would be, at least to a certain extent, analogical to that of humans. In fact, several studies, especially with rats and pigeons, revealed such similarities. As we have already learned, both rats and pigeons have been used as models of human cognitive aging (Bizon et al., 2012; Coppola et al., 2014), as they showed age-related decline in working memory which paralleled that of humans. This decline relied on the prefrontal cortex, the hippocampus, and the interaction between these two areas. In some delayed alternation tasks, rats with lesions to the prefrontal cortex showed impairment in both spontaneous and learned alternation between two arms (Wikmark, Divac, & Weiss, 1973; Divac, Wikmark, & Gade, 1975; Delatour & Gisquet-Verrier, 1996), revealing that they were no longer able to maintain the information on the already visited arm in working memory. And in some electrophysiological studies, rhesus monkeys, rats, pigeons and crows displayed neural activity in the prefrontal cortex/the nidopallium caudolaterale during the retention interval, revealing the "online" maintenance of the to-be-remembered information (Baeg et al., 2003; Browning, Overmier, & Colombo, 2011; Milimine, Watanabe, & Colombo, 2008; Rainer, Rao, & Miller, 1999; Rose & Colombo, 2005; Veit et al., 2014). Another study revealed a strong link between the rats' prefrontal cortex and the hippocampus, which was especially active before correct choices in a delayed-alternation task (Liu, Bai, Xia, & Tian, 2018), suggesting that the connection between these areas may be crucial for successful behavioural outcomes of the information processing in working memory. Likewise, the hippocampus itself was found to play an important role in working memory performance, as permanent lesions or inactivation of the hippocampus impaired rats' performance regardless of the retention interval (Bizon et al., 2012), and lesions to the hippocampal formation in pigeons (Colombo, Cawley, and Broadbent, 1997) and black-capped chickadees (Sherry & Vaccarino, 1989) impaired their performance on working memory tasks.

Mammalian, avian and human working memory seems to follow similar rules and rely on analogical neural principles (Balakhonov & Rose, 2017). But it seems that these memories have something else in common, too: they are capacity-limited and governed by chunking strategies. For instance, rats, when compared to humans in a 17-arm radial maze, showed the same working memory capacity of 5 to 9 items (Glassmann, Garvey, Elkins, Kasal, & Couillard, 1994; Olton, Collison, & Werz, 1977; Olton & Samuelson 1976). In two recent studies, the human-like capacity of four items was found in carrion crows (Balakhonov & Rose, 2017) and rhesus macaques (Buschman, Siegel, Roy, & Miller, 2011), although humans remain to be tested in the setup used in these two species. In another setup, rhesus macaques and pigeons were found to have a capacity of maximum one item, and humans of 2.5 items (Wright & Elmore, 2016). However, as mentioned above, comparing different species in a seemingly similar setup can be misleading, and yield results that will reflect the task differences rather than species differences in working memory. Some animals, such as rats, pigeons and rhesus macaques, have also been show chunk sequences of items into smaller portions (e.g., Fountain, 1990; Terrace, 1991; Scarf, Smith, Jaswal, Magnuson, & Terrace, 2018), and even alter performance in working memory tasks based on the records retrieved from long-term memory (e.g., Templer, Gazes, & Hampton, 2019).

How much does mammalian and avian working memory differ from that available to humans? According to Peter Carruthers (2013), there are at least eight different answers to this question, ranging from a complete lack of working memory abilities in animals to a qualitative difference between the contents of animal and human working memory. Before we move any further, let us briefly consider these answers in the light of the above-mentioned findings. (1) The first answer suggested that animals lack working memory abilities altogether, which seems highly unlikely, based on the above-mentioned studies. (2-3) The second and the third answer granted animals the access to working memory; the second limited the working memory capacity in animals to two chunks, and the third – to four chunks, but only in the absence of interference (Carruthers, 2013). It is difficult to discuss these two answers, as such capacity seemed to differ between tasks; at least in two experiments crows and macaques were found to have the human-like capacity of four items, but, on the one hand, humans have not been tested in an analogical setup yet, and, on the other, these experiments did not introduce interfering items that could restrict the working memory capacity. (4) The fourth answer admitted that animals could operate on information brought into working memory in a bottom-up way, but are not able to use top-down attention to bring back relevant records from long-term memory. This, again, seems highly unlikely, as some animals can use chunking strategies that rely on such records (e.g., Templer et al., 2019). (5) The fifth answer suggested that animals are not capable of "off-line" retrieval of the records of the past and so are not able to practice possible behavioural responses to the past situations. However, this answer, again, does not seem to be plausible, as we have already learned that at least some animals have the access to mind wandering that relies on the default mode network and allows them to, for instance, revisit a previously explored maze and even plot new routes that they will follow upon the next visit to the maze (e.g., Gupta, van der Meer, Touretzky, & Redish, 2010). This finding eliminates the sixth answer, (6) according to which, animals are not capable of transforming the retrieved records in working memory and organizing them into effective problem-solving sequences. This answer is also inconsistent with Clayton and colleagues' study with scrub-jays, in which the birds had to infer relative perishability of one familiar and one nonfamiliar item, based on the previous experience of the familiar item and another, now absent, one (Clayton et al., 2001). (7) The seventh, next-to-last answer suggested that animals can use working memory to a smaller extent than humans and only when they need to solve a certain task at hand; this answer could not hold, as at least some animals are capable of mind wandering, even though this mind wandering has no implications for the current immediate environment. This seventh answer is also inconsistent with some planning studies (Osvath & Osvath, 2008; Kabadayi & Osvath, 2017), in which animals needed to choose a certain tool that was not functional in the immediate context and required safe keeping for the eventual future situation. (8) The eighth and last answer postulated that animals and humans share and make frequent use of similar working memory abilities; however, the content of animal and human working memory is different, and the conceptual breadth of animals' working memory is more restricted than that of humans. Because animals lack the access to linguistic abilities, they also lack the verbal processing of the acquired information. This, in turn, must limit their reasoning and decision-making ability in some ways that call for further investigation.

Although many aspects of working memory have already been investigated in comparative setups, it seems that little, if anything, is known about the interplay between working memory and sociality across species. Sociality is thought to have driven the evolution of complex cognitive skills (for details see *Distant yet close*). As living in a social group requires keeping track not only of own, but also others' actions, working memory abilities may be especially pronounced in the social species. An attempt of initiating this line of research is described in Paper III; in this attempt, humans and ravens were, for the first time, compared in a novel experimental setup that allowed for simultaneous testing of working memory and sociality. Likewise, little is known about the way in which the attentional mechanisms chunk the perceptual input, and whether this chunking is revealed in observable behaviour. Therefore, in Paper IV another group of humans and the same population of ravens were tested in a novel decision-making setup that allowed for comparing the length of gazes in both species.

In this part of this introduction to the thesis, several aspects of animal memory were discussed and related to relevant aspects of human memory. We learned how the term of episodic memory was conceived and how it shaped the debate on the cognitive gap between animals and humans. This debate led to multiple studies of animal long-term memory and related cognitive capacities, ultimately expanding our knowledge of what and how animals may remember. In this part, we also found out why and how attention and working memory support long-term memory, and that the prefrontal cortex and the hippocampus play a crucial role in memory-driven responses to both immediate and delayed contexts. Putting together findings from psychology, animal cognition and computer modelling hopefully gives us a broader perspective on the papers gathered within this thesis. These papers report on empirical studies with great apes, Goffin's cockatoos, ravens and humans, that participated in certain experimental setups. All these setups had a comparative aspect, as one was tested with the great apes and the Goffin's cockatoos (Papers I – II), and two others were tested with humans and ravens (Papers III – IV). Although, by now, we would understand how these setups fit into the bigger picture of animal and human memory research, we might wonder why one would compare these particular species in the first place, and whether such comparisons make any sense. As we have already seen, testing two or more species with similar setups can yield results that may well tell us more about the task limitations than the cognitive limitations of the tested species.

Part 4. Why would one compare memory across species?

Different means, similar results

On the 3rd of March 2019, BBC Two, one of the British TV stations, broadcasted the first episode of a competition series called “Race Across the World”. The premise of the series is quite simple: the contestants race around the world to reach consecutive checkpoints, and ultimately arrive at a final destination before others do. They can choose any means of transport but a plane; they can also choose any route as long as they get where they were supposed to get, and they do that on time. To cut the long story short, the contestants’ goal can be reached in different ways and with different means, as long as those means serve the same function: of moving toward the goal. The contestants may take different roads, as long as they arrive at the same observable outcome, that is, physical presence in the desired location.

Throughout this introduction, we have learned that animals of different species may arrive at similar behavioural outcomes when tested in similar tasks. To reach subsequent locations in the “Race Across the World”, the competitors needed access to a certain limited pool of means that would eventually lead them to those locations. Likewise, to solve a given task, the animals need an access to a certain pool of cognitive capacities that would eventually allow for solving that task. Although the means of transport would serve the same function, they could look different: a ferry, a train, and a bus would have little in common visually, but they would all have some sort of engine and would all transport the passengers in the desired direction. This also applies to the cognitive capacities: although they all would serve the same function, they could rely on different-looking brain architectures that would share some sort of association between sensory and motor brain areas, and a central executive that would maintain the direction toward the goal. Investigating how animals with different brain architectures may have access to similar cognitive capacities, is a crucial step toward a better understanding of (1) which cognitive capacities are shared across various animal species (including humans), and which are not, (2) which mechanisms support common and specific cognitive capacities, and (3) how cognitive capacities may have evolved over time, reaching the current form.

Comparative studies of cognition in general, and memory specifically, can be conducted at least in two ways: in a top-down and a bottom-up way, following the analogical distinction to the one introduced in part 3. In the top-down mode of investigation, one uses tests of human cognition as the templates, gives them to animals, and reports whether the animals could perform on a par with the humans (cf. Emery, 2017). This top-down, anthropocentric approach, reiterates an outdated view of *scala naturae* – a hierarchy of animals with the simplest forms at the bottom and the most complex forms at the top (Hodos & Campbell, 1969; Emery, 2017), in which complex human cognition is a pinnacle of evolution, against which other species are compared. In this anthropocentric approach, different animal groups are usually compared with each other for the sake of emphasizing qualitative differences in their cognitive capacities and drawing sharp dividing lines between the worse and the better performing groups (De Waal & Ferrari, 2009). It does not matter how different animal species tackle similar challenges; it only matters which species can resolve these challenges, and which cannot. To avoid pitting some species against the other, one can choose the bottom-up mode of investigation instead. In this bottom-up, ecological approach, one confronts different animal species with ecologically valid tasks, that is, setups which resemble the challenges faced in the wild. The focus is shifted from whether the animal can perform on a par with the human to how and why the animal performs in a certain way. However, this approach to comparative studies is problematic as well. For instance, such studies tell us little on how animals tackle novel problems, and how flexible they are in responding to unfamiliar setups; and this approach does not allow for comparing species that live in vastly different habitats. In other words, while the top-down approach sacrifices the insight into cognitive capacities of specific species for the sake of comparison, the bottom-up approach sacrifices the comparability of performance across species for the sake of the insight into cognitive capacities of specific species.

The discussion of two contradictory and extreme approaches – the anthropocentric and the ecological one (cf. Emery, 2017) – sheds some light on generic problems of virtually all comparative behavioural studies. (1) First, they rarely can escape from transplanting terms used in psychological research with humans to animal cognition research (Chittka, Rossiter, Skorupski, & Fernando, 2012). This problem underpinned the debate between Tulving and Suddendorf on one side, and Clayton, Osvath and colleagues on the other, as the term of "episodic memory" was not only transplanted into animal cognition research under the slightly changed name of episodic-like memory, but even changed its definitions several times during the debate. The same critique could be obviously applied to this introduction to the thesis, and the papers that follow. However, it is difficult to escape from using established terms when reporting research results, as these results must be related to the bigger picture of the current state of knowledge in the field. To alleviate the problems that arise from using psychological terms in animal cognition studies, this introduction shows a variety of definitions and approaches to memory in general, and long-term and working memory specifically. All of these terms are used to describe certain constructs, and their definitions differ between fields and authors, which is not a perfect situation. However, the current thesis would only add to general confusion around these terms, if it proposed another nomenclature, that would not be grounded in the previous works. (2) Second, a certain task can play better into biological predispositions of some species than others and could therefore favour some species over others (Chittka et al., 2012). This is an important problem in comparative studies of cognition, which must be recognized and accounted for whenever two animal species are compared in a certain experimental setup. To compensate for this issue, one could confront the two species with a task that, while adjusted to the senses and motor abilities of the species, is somewhat artificial and perceptually different from the tasks encountered in the natural environments. In such situations, both species would suffer a certain disadvantage, but both would be in principle capable of perceiving and solving the task with the available appendages, such as hands, fingers, or beaks. (3) Third, when an animal fails a certain task, it does not necessarily mean that the animal does not have the prerequisite cognitive capacity; it might mean that some aspects of the task hinder accurate performance (Bitterman, 1965; Chittka et al., 2012). For instance, this was apparent when Mulcahy and Call (2006b) showed that the apes were more likely to succeed in the trap task, if they could rake, and not only push the reward; and likewise, when Seed and colleagues (2009) showed that the apes were more successful on a trap task when tool use was eliminated from the setup. (4) Fourth, using the results from comparative tasks to decide whether some cognitive traits were inherited from a common ancestor or evolved in two unrelated species can be misleading, as similar cognitive traits may either rely on similar or different mechanisms; to establish whether some cognitive traits evolved independently in two species, or were inherited from a common ancestor, the mechanisms behind cognitive traits must be investigated before any conclusions about the evolution of cognition are made (Chittka et al., 2012). To alleviate this issue, comparative behavioural studies can be supported by comparative studies of the underlying neural circuitry, and comparative genetic studies (e.g., Wirthlin et al., 2018). Although, in this thesis, only comparative behavioural studies were carried out, the other two branches of research would certainly help to pinpoint the cognitive mechanisms behind the behavioural performance in the compared species in the future.

Distant yet close

Despite the problems that come with comparative studies of cognition, these studies did not appear out of thin air. The memory studies carried out by Clayton and colleagues from 1997 onwards, showed that corvids paralleled primates in performance on similar memory tasks. Similar parallels were soon drawn in regard to biology, socioecology, behaviour and psychology of these animals (Emery, 2017). Both corvids and primates (1) were highly visual; (2) had appendages for fine manipulative actions (beaks and legs vs. hands and feet); lived in complex social groups, formed long-term alliances, and flexibly adapted own behavioural strategies to the current social context; (3) had a complex diet, and (4) seemed to share such cognitive capacities as flexible memory or means-end understanding, for instance, in the already-mentioned transfer studies. On top of that, both primates and corvids seemed to outperform other animals in cognitive tasks (e.g., MacLean et al., 2014, Kabadayi, Taylor, von Bayern, & Osvath, 2016). Soon this exclusive group of cognitively complex animals was joined by parrots that performed similarly to corvids in a range of cognitive tasks (Lambert, Jacobs, Osvath, & von Bayern, 2019) and, therefore, were supposed to possess similar cognitive capacities (Emery & Clayton, 2004, 2015; Emery, 2006; Güntürkün & Bugnyar, 2016; van Horik, Clayton, & Emery, 2012).

Although corvids, parrots and primates solve social and physical problems with similar speed and flexibility (Seed, Emery, & Clayton, 2009b), they reach similar behavioural outcomes with different means. These means serve the same function but look different: the avian brain of corvids and parrots looks different than the mammalian brain of great apes, but both brains contain some sort of a central executive and rely on common allometric principles (Güntürkün, 2012). At first glance, the avian and the mammalian brain have little in common, and even upon a slightly closer inspection, their forebrains vastly differ in terms of anatomic organization, which initially led to an assumption of profound differences between the more developed mammalian and the less developed avian brain (Edinger, Wallenberg, & Holmes, 1903). In mammals, the forebrain pallium consists mostly of a laminated cortex, but in birds, the forebrain pallium does not follow this laminar organization, and is organized in nuclei instead. Song birds, to which corvids belong, and parrots have smaller brains than primates in absolute terms (Olkowicz et al., 2016). However, in the recent years, these birds were found to have a higher packing density of pallial neurons compared to primates (Olkowicz et al., 2016), and to have relatively large brains for their body size. Therefore, regardless of the differences in organization of the pallium and absolute brain size, the brains of corvids, parrots and primates follow similar principles. These brains are relatively large for the body size, and the areas that are responsible for complex cognitive operations are disproportionally enlarged in corvids, parrots and primates. These enlarged areas consist of associative forebrain regions and mammalian striatum/avian striatopallidal complex (Stephan, Baron, & Frahm, 1988; Rehkämper, Frahm, & Zilles, 1991; Keverne, Martel, & Nevison, 1996; Barton & Harvey, 2000; Sol, Bacher, Reader, & Lefebvre, 2008; Mehlhorn, Rehkämper, Hunt, Gray, & Güntürkün, 2010; Güntürkün, 2012). Furthermore, both mammalian and avian brains include neuroanatomical equivalents of the central executive: the prefrontal cortex in mammals and the nidopallium caudolaterale in birds (Hartmann & Güntürkün, 1998; Güntürkün, 2005; Kirsch, Güntürkün, & Rose, 2008). Both of these areas share a range of anatomic, physiologic and functional similarities (Güntürkün, 2012), and they both mediate executive functions, crucial, for instance, for dealing with conflicts in both immediate and delayed contexts.

So far, we have learned that some complex cognitive capacities may be shared by corvids, parrots and primates, and could be unique to these groups, as they often outperform other birds and other mammals in various experimental setups. We have also learned which aspects of neuroanatomic organization are present in these groups and could support the information processing behind complex cognitive capacities. Just like comparing bodies and biological mechanisms of different animal species allows for figuring out how these species evolved over time, comparing their cognitive performance allows for finding out how cognition may have evolved, and ultimately, which claims of cognitive uniqueness in humans may be substantiated, and which may not.

Based on biological similarities and differences, all animal species are organized into so-called phylogenetic trees. The phylogenetic trees resemble family trees that list our family members - ancestors and descendants – and relationships between them. Likewise, the phylogenetic trees arrange different species into branches. Each branch starts with the last common ancestor of a given species and splits into the descendants, including this and all other species that likely came from the same ancestor species. Whenever an ancestor species splits into new ones in the phylogenetic tree, the two groups of descendants will share some common traits – sets of features – just like we share some traits with our siblings and cousins. However, sometimes species that shared the last common ancestor many, many branches ago, share common traits that were not retained from that last common ancestor. These traits evolved independently, when two animal species gained access to a similar solution in response to a common selection pressure. For instance, both sea lions and penguins have fin-like forelimbs that allow them to swim and forage under water, but their last common ancestor did not have such forelimbs. The forelimbs of sea lions and penguins were shaped by the selection pressure imposed by underwater environments. Although sea lions' and penguins' last common ancestor lived some 300 million years ago, their bodies converged on a similar solution in a similar environment, becoming an example of so-called convergent evolution. By analogy, although the last common ancestor of birds and mammals lived some 300 million years ago, the cognitive capacities of these groups may have likewise converged in response to similar environmental challenges.

Several environmental challenges, that could have driven the evolution of complex cognition, may be common for primates, corvids and parrots. These pressures could pertain to the physical environment, in which the animal forages, and to the social environment, in which it interacts with conspecifics. The first challenge was identified as seasonal variability and dispersion of food resources (Milton, 1981). Primates, for instance, rely on tropical plants, which are patchily distributed in the rainforest and only seasonally provide edible food items. As, over time, individuals could learn where and when these items would appear, they could have developed efficient foraging strategies that required complex levels of memory and planning. This might have been the case for parrots, too; and while corvids inhabit a much wider spectrum of habitats – from temperate to desert – they likewise learned to deal with the seasonal abundance of food; their strategy involves caching the food in multiple locations in the periods of availability, and retrieving it later, when the availability drops (Pravosudov & Roth, 2013). Primates, corvids and parrots are also often dietary generalists and extractive foragers; this means that they eat a range of different food items, both plant-based and animal-based, that require, for instance, digging in different substrates or cracking hard-shelled items open. As extracting these items may even require multi-step, hierarchically organized strategies and tool use, relying on such a diet could have supported the emergence of means-end understanding and active selection of some behavioural goals over the other, and executive control of fulfilling multi-goal action sequences. Primate, corvid and parrot cognition may have also been shaped by the demands of living in a complex social group, such as engaging in competitive and cooperative interactions, and learning from observing how other members of the social group solve various problems (e.g., Aureli et al., 2008; Szipl, Ringler, & Bugnyar, 2018). Keeping track of own and others' actions, both with respect to food resources and social interactions, is crucial for adjusting own behavioural strategies to the rapidly changing physical and social landscape. These strategies may not only rely on well-developed long-term memory, but also executive control over behavioural responses to the actions of different members of the social group. As such groups are usually hierarchically organized, the animals must remember who is who in the group, and, for instance, refrain from some actions towards the animals that are higher in the hierarchy to avoid repercussions, or form alliances with the powerful in the group. Living in a complex physical and social environment requires a great deal of behavioural flexibility, as the animal must adapt to a range of rapidly changing physical and social circumstances by switching between diverse goal-appropriate strategies.

The access to complex cognitive capacities, that afford flexible behaviours, comes at a cost: on one hand, these capacities require time-consuming development and learning, and on the other, they require information processing that consumes a lot of energy which could otherwise go into foraging or reproduction (e.g., Seed et al., 2009b). Therefore, for complex cognitive capacities to evolve, having them must have, under certain circumstances, outweighed the related time and energy costs. Peter Godfrey-Smith (2001) and Kim Sterelny (2003) suggested that only living in an unstable, ever-changing environment could have inverted the unfavourable expense ratio of the complex cognitive capacities and allow for them to evolve. Therefore, behavioural flexibility might have been driven by environmental complexity and variability (Seed et al., 2009b). However, such behavioural flexibility might have, as well, originally evolved under other selective pressures, and later allowed for taking over complex and variable environments. In immediate contexts, such behavioural flexibility is supported by efficient information processing in attention and working memory, as the animal must select and pursue some more important goals over the less important ones. However, this flexibility can be further boosted by selective retrieval of information from long-term memory and recombining it into innovative solutions to novel problems. Whether animals, that are currently considered as cognitively complex, are capable of such combinatorial flexibility, calls for further investigation. Hopefully, future investigations could draw on some ideas put forth in this thesis.

Part 5. Which studies were carried out within this thesis?

This introduction is followed by four reports from empirical studies. The studies reported in Papers I and II involved great apes and Goffin's cockatoos and addressed the combinatorial flexibility within their long-term memory. The studies reported in Papers III and IV involved humans and ravens; Paper III addressed the interplay of memory and sociality in the context of caching, and Paper IV addressed the role of attention in information processing and behavioural segmentation, in the context of simple decision making. Short summaries of these papers are available below.

Paper I

Great apes resolve competition between conflicting memories and selectively retrieve relevant memories to guide action

Memory allows us to draw on past experiences to inform behavior in the present. When the past guides actions, memories rarely match exactly the situation at hand, and new situations regularly trigger multiple related memories where only some are relevant to act upon. The flexibility of human memory systems is largely attributed to the ability to disregard irrelevant, but salient, memories in favor of relevant ones. This is considered an expression of an executive function associated with the prefrontal cortex. It is unclear to what extent animals have access to this ability. Here we demonstrate that great apes suffer conflict between memories, and that they are able to resolve this conflict by selecting relevant memories over competing yet irrelevant ones. Such mnemonic flexibility is among the most advanced expressions of executive function shown in animals to date and might explain several behaviors related to tool-use, innovation, planning and more.

Paper II

Goffin’s cockatoos *(Cacatua goffiniana)* can use conflicting past experiences to solve a novel problem

Novel problems often partially overlap with familiar ones. Some of their features match the features of previous situations stored in long-term memories and therefore trigger their retrieval. Such memories can overlap in different ways with the current problem; for instance, they may share a visual or mechanistic similarity. When the visually similar memory is irrelevant for the correct solution, another, functionally relevant memory should be selected instead. Selecting relevant over irrelevant memories is a hallmark of behavioural flexibility in humans, and has recently been shown in great apes. However, it is unclear whether any species that are distantly related to us are capable of such memory recombination. As recombining familiar solutions in the face of novel problems has been linked to technical innovativeness, other highly innovative species may also have access to the capacity. In the current study, we show that Goffin’s cockatoos, an innovative tool-using bird species, use previous experiences to solve novel, partially overlapping problems, and also selectively recombine relevant and irrelevant experiences when doing so. The result supports the hypothesis that technical innovations depend on flexible memory functions.

Paper III

Social context motivates ravens but hinders humans in a short-term memory task

Using resources shared within a social group – either in a cooperative or a competitive way - requires keeping track of own and others’ actions, which, in turn, requires well-developed short-term memory. Although short-term memory has been tested in social mammal species, little is known about this capacity in highly social birds, such as ravens. We compared ravens (*Corvus corax*) with humans in spatial tasks based on caching, which required short-term memory of the actions of others. Human short-term memory has been most extensively tested of all social mammal species, hence providing an informative benchmark for the ravens. A recent study on another corvid species *(Corvus corone)* suggests their capacity to be similar to the humans’, but short-term memory skills have, to date, not been compared in a social setting. We used spatial set-ups based on caches of foods or objects, divided into individual and social conditions with two different spatial arrangements of caches (in a row or a 3x3 matrix). In each trial, a set of three up to nine caches was presented to an individual that was thereafter allowed to retrieve all items. Humans had better scores on average across trials. However, the ravens performed relatively better than the humans, when they had to keep track of a partner's actions; and contrary to the humans, the ravens only maximized their success in those conditions. That is, they were better in the social than in the individual conditions, while the opposite was true for humans. It appeared as if the social context was more motivating for the ravens leading to better attention towards the task. The tasks had a competitive element, and one might speculate that ravens' attention and memory strategies are more attuned to such situations, in particular in caching contexts, than is the case for humans.

Paper IV

Cognition in the fast lane: Ravens' gazes are half as short as humans' when choosing objects

Time cannot be directly perceived; instead, its flow is inferred from the influx of sensory information. To prevent sensory overload, attentional mechanisms split up information into processable units. This portioning remains imperceptible to the individual. However, the length of these units still influences the speed of perception and the speed at which behaviors are performed. Previous studies have focused on establishing the length of these units in various mammalian species – mainly humans – by measuring different types of behaviors, including gaze. However, no such studies have been conducted on birds. We measured duration of ravens' (*Corvus corax*) single gazes towards selectable objects before a choice was made, and compared it with that of humans in a similar set up. The raven gaze durations were approximately half those of humans (which fell slightly short of previously established ranges). We hypothesize that these differences are mainly due to the much higher so-called flicker-fusion-frequency in birds, which makes their vision faster in the sense that it picks up more information per time unit than mammalian vision does. We further discuss that the speed of perception might influence the general speed of cognitive processing in more complex tasks as well, and suggest that the addition of a temporal component in comparative cognitive studies might be informative.

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