

From the Messerli Research Institute  
University of Veterinary Medicine, Vienna

Unit of Comparative Cognition

(Head: Univ.-Prof. Mag. Dr. Ludwig Huber)

## **Sequential Learning in Kea (*Nestor notabilis*)**

Master Thesis

University of Veterinary Medicine

Interdisciplinary Master in Human and Animal Interactions

Master thesis submitted for the fulfilment of the requirements for the degree of

Master of Science (M.Sc.)

Submitted by

Adele Tuozi, BSc

Vienna, April 2021

Supervisor: Raoul Schwing, PhD

## **Acknowledgement**

I would like to thank my supervisor Raoul Schwing for his guidance and help on this project, for inspiring me as a scientist and for making possible the incredible experience to work with kea parrots.

I would like to thank my colleagues Catherine Cords and Max Benatar for the great teamwork at the beginning of this project.

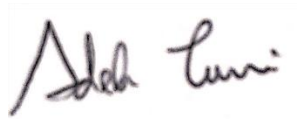
Furthermore, I would like to thank Phin Anibal for his help and the team at the research station Haidlhof for the great work and for helping me and teaching me how to interact with the kea.

Finally, I would like to thank all the kea that took part in this project and that made this experience unforgettable.

## **Plagiarism disclaimer**

I declare that this thesis is my own and autonomous work. All sources and aids used have been indicated as such. All text quoted directly or paraphrased have been indicated by in-text citations. Full bibliographic details are given in the reference list. This work has not been submitted to any other examination authority.

Signed,

A handwritten signature in black ink, appearing to read 'Adele Tuozi', written in a cursive style.

Adele Tuozi, 18.03.2021, Vienna, Austria.

## Table of Contents

<b>1. Introduction</b> .....	- 1 -
1.1 Previous studies on sequential learning .....	- 1 -
1.2 Levels of sequential learning .....	- 3 -
1.3 Chunking .....	- 4 -
1.3 Spatial Ordinality .....	- 5 -
1.3 Sequential learning in animals .....	- 5 -
<b>2. Material and methods</b> .....	- 10 -
2.1 Test subjects .....	- 10 -
2.2. Test apparatus .....	- 11 -
2.3. Procedure .....	- 13 -
2.3.1. Setting .....	- 13 -
2.3.2 Training .....	- 15 -
2.3.3 Testing .....	- 17 -
2.4. Data collection .....	- 19 -
2.5. Statistical analysis .....	- 19 -
<b>3. Results</b> .....	- 20 -
<b>4. Discussion</b> .....	- 28 -
<b>5. Summary (EN)</b> .....	- 34 -
<b>6. Zusammenfassung (DE)</b> .....	- 35 -
<b>References</b> .....	- 36 -
<b>List of figures</b> .....	- 44 -
<b>List of tables</b> .....	- 45 -

## **1. Introduction**

Sequential learning, or the cognitive process of learning the proper order of events or stimuli (Conway, 2012), is also defined as “the ability to encode and represent the order of discrete items occurring in a sequence” (Conway & Christiansen, 2001). It refers to any task that requires creating an association between items in a sequence and putting them into an ordered series through the performance of a behavioural sequence (Inoue & Matsuzawa, 2009). It also refers to anticipating events that occur in a consistent sequential order (Fountain, 2008). Another possible definition of sequential learning is the ability to learn underlying structured patterns that exist among a set of non-random, sequentially presented stimuli (Conway, 2012; Conway & Christiansen, 2001). The ability of sequencing information is fundamental in humans (Clegg et al., 1998) and animals. It is applied in a considerable variety of actions, both physical and mental, as visual scene analysis and motor learning (Milne et al., 2018). In humans, the most explicit example of use of sequences is in the acquisition, development and use of language (Conway et al., 2007). Other examples, which seem to be simple and automatic actions, involve processes of sequential learning, such as dialling a phone number or tying shoes. Sequential learning is also characterized by a temporal component, playing a role in the ability to remember specific events from the past and specific sets of relationships among events. This ability is applied in many behaviours that require the prediction of future events. Also, the ability to learn about temporal patterns and make predictions about upcoming events is necessary in an ecological context (Daltrozzo & Conway, 2014). Thus, sequential learning is essential to predict seriality in events in the animal’s environment and therefore essential for its survival (Milne et al., 2018). The feature of a serial order in behaviour is fundamental for both humans and animals to solve an enormous number of tasks. Therefore, sequential learning represents one of the most prevalent forms of human and animal learning (Sun, 2001).

### **1.1. Previous studies on sequential learning**

The question about what is learned in sequential learning and how the mechanism of information acquisition in sequential learning works has been long investigated in research, and many questions remain unanswered. In 1951, Lashley published a paper titled “The problem of

serial order in behaviour”, which was one of the first papers to address the importance of sequences in learning in the field of cognition (Lashley, 1951). Lashley widely discussed the importance of sequencing in human behaviour, especially in the use of language. For example, the way the order of the words inside a sentence influences its final meaning. The earlier interpretation of non-human serial learning mechanisms were analysed in the context of association of stimuli and responses (Hulse & Dorsky, 1977). Some of the first studies to bring attention to the specific mechanism of sequential learning in animals are dated in the 70s and 80s (Capaldi & Molina, 1979; Haggbloom, 1985; Restle & Burnside, 1972; Roitblat et al., 1983; Straub et al., 1979). During these years the most relevant work on the topic was done by Stewart Hulse and colleagues, specifically on serial pattern learning in rats (Fountain et al., 1983; S. B. Fountain & Hulse, 1981; Hulse & Campbell, 1975; Hulse & Dorsky, 1977, 1979; Hulse & O’Leary, 1982). Their work consisted of analysing if rats were able to learn to anticipate a series of different food quantities presented in a runway and consequently about the structure and organization of a sequence. They concluded that the rats demonstrated a rule-learning theory following some representation of the abstract rules on which sequences are organized (Muller & Fountain, 2010), and that they did not have to rely on chaining or remote associations alone to manage the sequences (Fountain, 2008). In general, in the beginning the studies on sequential learning focused more on “chaining”, where sequences were considered simply associations between adjacent items, while later on, knowledge on ordinal and spatial position of items were added to this chaining theory, describing the relationship between them even when they were not next to each other (Terrace, 2010).

During the 90s, most of the psychological studies on sequential behaviour were focused on the memorization of syllables as well as the solving of various types of mazes, leading to the conceptualization of serially organized behaviour as a linear sequence of associations (Fountain et al., 2002). The beginning of exploration regarding the mechanisms of sequential learning in animals started with the development of models that did not involve direct use of language. A relevant work in this case was made by Restle and Brown in 1970, who developed a model to study serial patterns in humans via a non-verbal task that could be adapted for animals, pre-verbal infants, and humans with language disorders (Garlick et al., 2017; Restle & Brown, 1970). The model was based on a six light matrix arranged in a row with six complementary buttons. The subjects were required to make repeated choices from the buttons, and if their

choice was correct, a feedback would be given by the light above the button they selected. In this way, it was possible to test if the subjects were sensitive to some pattern in the sequences. Thus, this study represented one of the main blocks on which the study of sequential learning in animals is now based.

One of the most common models to study sequential learning is represented by the Serial Reaction Time Task (SRTT), developed in 1987 by Mary Jo Nissen and Peter Bullemer to study sequential learning reactions in human (Nissen & Bullemer, 1987). This model is widely used to study implicit sequence learning, which is when the learning process occurs without awareness. It represents a simple paradigm on which much of the research on sequential learning is founded, and in the next two decades it would become an essential tool in understand the underlying mechanism of spatial sequential learning (Schwarb & Schumacher, 2012). The original task consisted of four cues appearing in four possible different locations horizontally aligned on a monitor. The subject had to push one of the four correspondent response buttons situated under the cue's positions. After pushing the button, the cue would disappear, concluding the trial. The next trial would then start with a new cue. The subjects were divided in two groups, one of which would encounter a repeating sequence, meaning that the first 10 trials positions of the cues would repeat as a continuous series. For the other group, the positions of the cues were randomized for each trial, however the cues were arranged so that they would never appear in the same position in two consecutive trials. The subjects in the repeating sequence group reacted faster and made less errors compared to those in the randomized group (Nissen & Bullemer, 1987). This is the standard sequential learning effect, which tell us that the subjects learned something about a list and that sequence learning depends of the structure of the sequence (Schwarb & Schumacher, 2012). From this first model, the SRTT has been modified and adjusted to answer specific questions, but it remains a valid and clean example to study sequential learning, especially when the serially ordered stimuli are not cued. The SRTT is also used as a model to study sequential learning in animals. Modifications of the model have been used in different species.

## **1.2. Levels of sequential learning**

On the structural level, sequential learning can be differentiated in three models: fixed, statistical and hierarchical. Fixed sequential learning is the simplest structure, in which a



sequence is composed by arbitrary fixed elements (Conway & Christiansen, 2001). A classic example of this is the written word. The letters composing words have a fixed order to give them a meaning, and a different sequence of letters would form a different word. Rather than having fixed elements in a sequence, statistical (also known as probabilistic) learning involves the combination of items that frequently occur together in patterns (Christiansen, 2019). In keeping with the use of language as an example, it is possible to predict which elements will complete a word after hearing the first syllable. Other examples include that of learning the basic rhythms of different kinds of music or the basic steps of a dance. Animals can learn statistical patterns recurring in their environment to predict events (Kelly & Martin, 1994). Hierarchical learning is characterized by the relationships between items which are non-adjacent and non-consecutive within a sequence. Simple elements are combined to form more complex structures which are called “chunks”, which then represent the hierarchical structure.

### **1.3.Chunking**

One of the most relevant cognitive processes involved in sequential learning is therefore known as “chunking”. This is the act of dividing and segmenting a sequence into smaller blocks. A chunk represents a piece of information containing elements that have a strong association with one another, but weaker associations with other chunks (Gobet et al., 2001). Chunking is a fundamental attribute of learning and working memory (Isbilen et al., 2020; Sakai et al., 2003). By segmenting a sequence into chunks, it becomes easier to retain and recall the correct order of the sequence (Fonollosa et al., 2015). Chunking mechanisms thus play a fundamental role in sequential and statistical learning. The information carried in the chunk is contingent among the structure of a sequence, and the distribution of elements can influence the learning task, for example putting the frequent occurrence of grouped elements in a stream of information in a coherent unit (Isbilen et al., 2020). To clarify the concept with a familiar example, let’s consider the structure of a sentence. In a sentence, some letters frequently occur together, creating the words; these words represent chunks inside the sequence of the letters which form the whole sentence. Language acquisition has been shown to include similar processes among the necessary learning skills (Christiansen & Chater, 2016). The theory that chunking mechanisms play a role in learning is supported by models as the chunk-based learner model (CBL), supports the fact that language acquisition comprehension and production is based on slowly

incorporated units that gradually build the language inventory (McCauley & Christiansen, 2019). The use of chunks is a topic that has also been studied in animals since the start of animal sequential learning research. Many studies explored and hypothesized how animals chunk and rank information during learning and memorization processes (Wallace & Fountain, 2002). According to these studies, animals are able to chunk information and hierarchically arrange it to ease sequential learning and memory (Dallal & Meck, 1990; Terrace, 1987; Wallace & Fountain, 2002).

#### **1.4. Spatial Ordinality**

Spatial ordinality is the mechanism of encoding the position of the items inside a sequence and understanding their relative position to one another in space. Thus, it represents a driver for learning speed (Chen et al., 1997; Endress et al., 2010). In this case, a sequence is not anymore learned through the chaining of elements, but through a mechanism of remembering that the first element is in a certain position, the second is in another, and so on. This represents an abstract coding (Endress et al., 2010). Elements in this case occupy a specific place and are encoded by their ordinal position among the sequence instead of being associated by the consecutive items in the sequence.

#### **1.5. Sequential learning in animals**

In general, many models to investigate the presence of serial pattern learning have been created and described in different fields as cognition, psychology, and animal behaviour. For the latter, the main questions are if relational structures inside a sequence can influence how and what animals learn about it. Sequential learning has been studied on a various number of species. On the simpler level of fixed sequences, it has been observed that chimpanzees (*Pan troglodytes*) are able to learn an arbitrary four-action fixed sequence simulating natural sequential feeding behaviour on an artificial fruit (Whiten, 1998; Whiten et al., 1996). Zebrafishes (*Danio rerio*) use both spatial and ordinal (numerical) information to maximize their success in localizing a target (Potrich et al., 2019). Cotton-top tamarins (*Saguinus oedipus*) are able to chain different elements in a sequence (Locurto et al., 2013).

Many studies have observed how animals can be sensitive to the local structure of a sequence, or chunks, in sequential pattern learning. In a series of interesting studies on the Serial Multiple

Choice (SMC) task, first developed by Fountain and Rowan in 1995, rats were introduced to an octagonal chamber and required to press 2 levers in a specific order with different patterns, using different kind of chunks (Fountain & Rowan, 1995). The study found that different patterns influenced the performance of the rats. In 2017, Garlick and colleagues used the SMC task to study sequential learning in pigeons (Garlick et al., 2017). This time a touchscreen was used, and instead of levers, two circles would light up. Again, the way the sequences of stimuli were presented followed different structure patterns. At the easiest level, which had two choices, they found that sequence behaviour in pigeons was controlled by low-level cues, such as through associative learning rather than serial-pattern learning. At the level with three choices, the mechanism that regulated the pigeons' choices was observed to be a spatial cue; the physical position of the stimulus itself. When they moved to an eight positions choice and randomized the position of the beginning of the sequence, they found evidence of rule-learning in pigeons, indicating that pigeons are able to abstract the higher-order structure of a repeating sequence. Furthermore, on the basis of the SRT by Nissen and Bullemer described above, pigeons were also observed to be sensitive to the local structure of a sequence (Froehlich et al., 2004). The pigeons were tested in two condition involving either a structured or a random sequence of nine illuminated spatial locations. Each trial consisted of a response-to-stimulus (RS) interval in which the pigeons were trained to peck the illuminated light, which would remain on until touched. The results show that the more "predictable" a location of the cue is, given the previous one or two locations, the faster the response to it would be, contrary to a total random position of the cues. Both experiments confirm that pigeons are able to extract local statistical information from a repetitive sequence of events, and to use that information to respond adaptively to a spatial location (Froehlich et al., 2004).

Spatial ordinality has been demonstrated in non-human primates, with macaque monkeys and chimpanzees applying this concept to learn the sequence of items in a list. The work by Chen et al. on rhesus monkeys (*Macaca mulatta*) demonstrates this concept well: the subjects were trained to learn a list of different items (coloured pictures), each of which were randomly positioned on a touchscreen. Sequentially, the subjects were exposed to novel lists, which contained some of the same pictures as the original, but a different spatial combination. Singular items in some derived lists maintained the same position as in the original list, while in others the position of the items was always different. The monkeys learned the lists that maintained

the ordinal position of items much faster than the novel lists, showing that they learned that ordinal position of the a specific item and use of information as a strategy for sequential learning (Chen et al., 1997). Later studies confirmed that rhesus macaques reproduce sequences of items by relying on the memory of each item's ordinal position rather than on chaining or forming associations between adjacent items on a list (Terrace et al., 2003). The same phenomenon of utilizing spatial cues while learning a list has been observed in pigeons (Scarf & Colombo, 2011). Ring-tailed lemurs (*Lemur catta*) can encode a spatial sequence based on ordinal cues (Drucker et al., 2016). Birds have also demonstrated such learning strategies, as jackdaws (*Corvus monedula*) have been observed to have a concept of ordinal position when trained on a series of sequences composed by the three items of one triplet when presented in fixed order (Pfuhl & Biegler, 2012).

In general, one of the most interesting questions that sequential learning studies aim to answer are which mechanism is used by animals to learn sequences and in which different species. Most of the studies on chunking or spatial ordinality focus specifically on a singular mechanism. One of the most relevant studies made on the topic is by Inoue and Matsuzawa (2009), in which an original arrangement of a sequence was used, with the goal to describe how chimpanzees with no previous experience learned the sequential order of numerical items and to determinate the nature of the chimps' knowledge of acquired order (Inoue & Matsuzawa, 2009). The subjects, 6 chimpanzees, were trained on an Arabic numeral sequence from 1 to 9. The items of the sequence were non-adjacent, and in a random position in every trial, and the subjects were required to touch the numerals on a touch screen in ascending order. Every time a numeral was selected correctly it would disappear from the monitor. At the end of a full correct sequence the subject was rewarded. Before the test itself, the chimps were trained to touch every number at a time. First, the number 1 would appear in different positions on the screen and the chimps learned to touch it in order to obtain a reward. After reaching a certain criteria, the number 2 was added, appearing as sequence made of 1-2, which had to be touched in the right order to obtain a reward. Then the number 3 would be added, and consequently all the numbers until 9, at which point the chimps had learned the whole sequence step by step from 1 to 9. All the chimps managed to learn the full sequence from 1 to 9 in ascending order, and the response time was longer for the first number, while equal for numbers after it regardless of the length of the sequence, revealing a possible pre-planning strategy. The same experimental

setting was also applied to a gorilla, Rollie, (*Gorilla gorilla gorilla*) by Ross (Ross, 2009) confirming that the subject was also able to learn a list of 9 items in ascending order.

What would represent an interesting setting is to use a sequence of items consisting in separate actions to understand which mechanisms are in use during animal sequential learning. Combining the 9-step structure used in the study by Inoue and Matsuzawa to touching a fixed order but with no difference in the items would exclude the possibility that what is learned is the item itself. Furthermore, by leaving the sequences visible without making the correctly touched items disappear (as in a Simultaneous Chain setting) the subjects' choices are not limited. Keeping sequences visible and also rewarding subjects at the end of the trial (as in Serial Reaction Time Task) could allow us to explore which mechanisms are applied to learn the sequences.

### **Can Kea learn a complex sequence?**

The present study aimed to explore the question whether kea parrots are able to learn a complex sequence. Kea are an endemic parrot species of New Zealand, living in alpine environment of the Southern Alps (Diamond & Bond, 1999). Kea are highly neophilic, and have great innovation scores which seem to parallel great apes in some performances (Auersperg et al., 2011; Huber & Gajdon, 2006). Kea have succeeded in tasks that required a sequential series of different actions to obtain a reward, such as manipulating a box that that needed various type of manipulation to extract a food reward (Huber et al., 2001), and using a tool in a task-directed action (Auersperg et al., 2011). Furthermore, kea were able to generalize learned rules to novel stimuli in a task that required them to discriminate between stimuli following two different patterns (Stobbe et al., 2012). Consequently, Kea seem to be a promising species to study the mechanism underlying sequential learning. We hypothesized that Kea are able to focus on a sequence of steps without a difference in the type of action required. The stimulus used to learn the sequence will thus remain uniform. Also, we hypothesized that the arrangement of the sequence can affect the kea's learning speed. We also hypothesized that kea are able to rely on spatial rules and chunking mechanisms to remember a complex sequence of actions. To test these hypotheses, we used two different sequences, one with a linear structure, in which a chunking pattern was repeated three times, and the other with a random structure, in which there were no fixed rules concerning the position of the stimulus. If both our hypotheses are true, the

Kea should learn the linear sequence faster in the linear condition than in the random condition. If the Kea rely on chunking mechanisms to learn the sequence, the learning speed should increase after learning the first fixed chunk pattern in the linear sequence. If the Kea rely on spatial rules to learn the sequence, there will be no difference in the learning speed in the different chunks of a subsequence. The kind of sequences used in this experiment include elements from the SRT, such as the cues without difference, as well as elements from the simultaneous chain because all the stimuli of the sequence are presented together to the subjects. The two differences in the arrangements of the sequence will allow us to investigate which mechanisms are used by the Kea to learn the sequence (chunking, or spatial ordinality).

## 2. Material and methods

### 2.1 Test subjects

The experiment was carried out with 10 captive individuals of *N.notabilis* (see table1) at the Haidlhof Research Station (Austria). The animals were kept in a social group of 26 individuals in a large aviary, measuring 52m x 10m x 4m, which was abundantly environmentally enriched. It was possible to isolate 9 different areas of the aviary with sliding gates: two breeding areas, three main living areas, and two testing areas that can be subdivided into waiting and testing areas. In addition, the different areas can be visually isolated by solid white sliding panels. The aviary was provided with hiding opportunities, artificial ponds, perches, plants, and others various elements as enrichments. Water was provided *ad libitum* and the birds were fed 3 times a day in accordance with their nutritional requirements and were never food deprived for testing purposes. The birds were weighted on a weekly basis to assess their nutritional needs. The kea participating the studies were 6 males and 4 females, all between 2 and 18 years old (see Tab. 1). One of the subjects, Elvira, was dropped during the experiment because of health reasons.

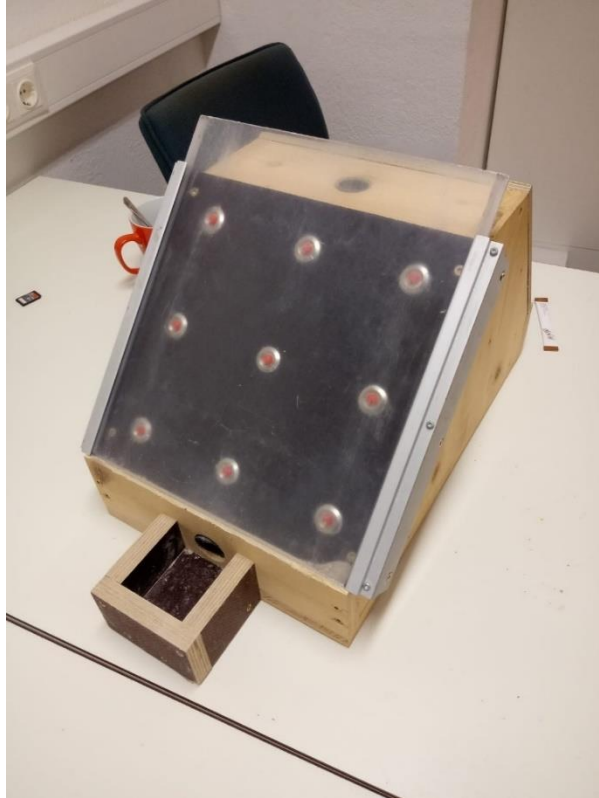
*Table 1. Individuals participating the experiment with their name, age at test time, sex, modality of rearing and correspondent sequence group of the test.*

<b>Name</b>	<b>Age at test time</b>	<b>Parent/hand reared</b>	<b>Sex</b>	<b>Testing group</b>
Mali	4	parent	Female	Linear 1
Odo	3	parent	Male	Linear 1
Sunny	11	hand	Female	Linear 1
Paul	8	parent	Male	Linear 2
Kermit	14	hand	Male	Linear 2
Roku	10	parent	Male	Random 1
Pick	14	hand	Male	Random 1
Elvira	18	parent	Female	Random 2
Fay	2	parent	Female	Random 2
Jean-Luc	3	hand	Male	Random 2

## 2.2. Test apparatus

A wooden apparatus with 9 LED lights was used for this experiment (see figure 1 and 2). The lights were positioned on the front panel, affixed in a 3x3 matrix with equal distance between each other. On the back panel of the apparatus were 9 corresponding buttons that could operate all individual LED's. A Plexiglas cover was positioned on the front side of the apparatus, where the lights were, to prevent the birds from touching them when there were not meant to be interacting with the lights. The Plexiglass cover could be easily removed and replaced as it was made to slide into the front part of the apparatus. To present the focal bird with a reward while avoiding the possible influence of direct contact between the bird and the experimenter, a tube was built inside the apparatus, running from the top of the apparatus to the bottom part, where it ended with a small container. This allowed the experimenter to drop the reward through the tube so that it would land in front of the bird. The reward consisted in 1/8 of a peanut.





*Figure 1. Front part of the apparatus used in the test. This side is the one presented to the kea, with the nine LED lights and the Plexiglas cover on. After the subject entered the testing area, the sequence would be presented to the bird with the Plexiglas covering in place. After the sequence was presented, the Plexiglas cover would be lifted, and the kea would be able to touch the lights. If the trial was successful, the reward would then be inserted manually by the experimenter into the hole in the upper part of the apparatus, where it would slide along the tube to be collected by the bird. If the trial was unsuccessful, the Plexiglas cover would be positioned in the apparatus again and the bird would exit the testing area without reward. ©P.Anib*



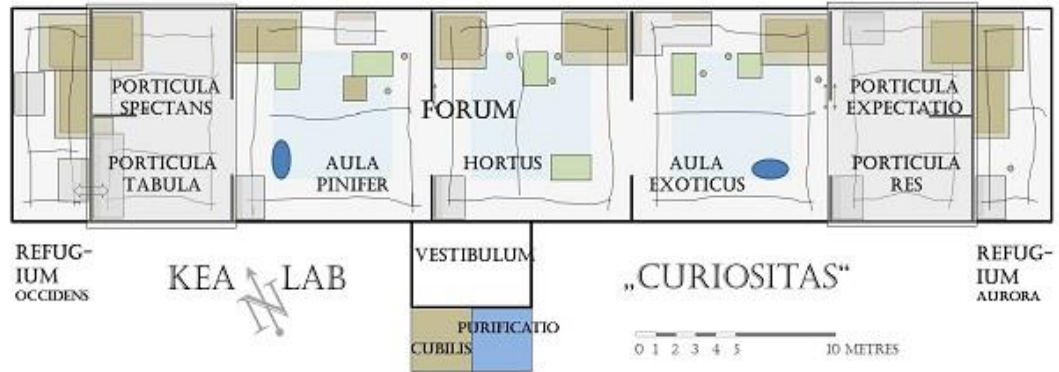
Figure 2. Back part of the apparatus, on the experimenter's side, where the nine buttons corresponding to the nine lights are placed. The hole where the rewards are placed is visible, as are the cables used to charge the battery of the apparatus. © P.Anibal

## 2.3. Procedure

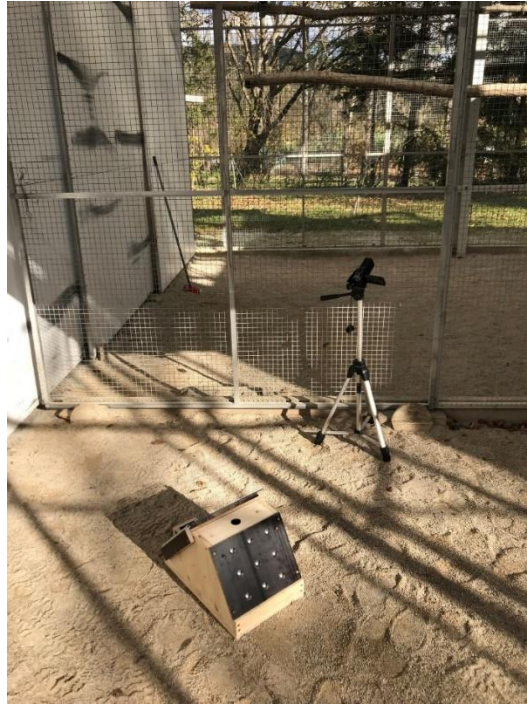
### 2.3.1. Setting

The experimental part of the project took place between October 2018 and September 2019, three days each week. Training and testing were done in the morning (10.00 am – 12.00 pm) and the afternoon (1.30 pm – 3.30 pm). The testing compartment “*Porticula Res*” (see figure 3) was located on the side of the aviary, and before starting the testing it was isolated from the other compartment with the sliding white panels to prevent the birds in the aviary from observing the other birds in the testing area. The apparatus was placed in the direction of the testing area entrance to be seen by the bird (see figure 4). The tested bird was called singularly into the adjacent waiting area “*Porticula expectatio*” before entering the testing compartment

and starting the test. The birds entered the waiting and testing compartments voluntarily. Between every trial, the focal bird returned to the waiting area to allow the experimenter to prepare the apparatus for the next trial.



*Figure 3. The aviary's different areas. The experiment was carried on in the Porticula Res, while the Porticula Expectatio had the function of waiting area for the birds. Both the tasting and the waiting area were visually isolated to prevent social learning.*



*Figure 4. The experiment setting: the apparatus seen from the experimenter's perspective inside the testing area, with the camera to record the results. The gate separates the waiting area from the testing compartment. The white panels visually isolate the whole area from the rest of the aviary. © A.Tuozzi*

### 2.3.2 Training

The goal of the training was to make the birds familiar with the apparatus and teach them to touch a light when it was turned on by the experimenter in order to obtain a reward. The training consisting in 4 different phases and was introduced to the birds before starting the test.

*Table 2 Description and goal of every phase of the test.*

<b>Training phase</b>	<b>Method</b>	<b>Goal of the phase</b>
<b>Phase 1</b>	The experimenter lit a random light until the kea touched it with their beak to get a reward.	Subject associates activated LED with reward.
<b>Phase 2</b>	The first light touched by the bird had to be the one lit up. The birds learned that only their first touch was correct and rewarded.	Subject associates first touch with reward
<b>Phase 3</b>	The Plexiglas cover was introduced: it covered the front panel and the birds had to wait for the experimenter to remove it before they could touch the light that was lit up behind it to be rewarded.	Familiarisation with the cover
<b>Phase 4</b>	The experimenter turned off the light before the Plexiglas cover was removed. The birds had to memorise which light was turned on and touch it to be rewarded.	Memorisation of position of activated LED

Each session for bird consisted of 10 trials. To move to the next training phase the bird had to complete two consecutive sessions with 100 % correct trials.

### 2.3.3 Testing

After a subject completed all the four phases of the training, the actual testing sequence was presented. The birds were divided in two main groups based on the sequence they would perform (see figure 5). The groups were:

- “Linear”: the sequence follows a linear pattern, with the cues (the lights) one next to each other on the 3 rows. Every line represents a chunk of the sequence that follows the same pattern. The first cue of every line starts on the same side of the other lines. The linear group is further divided in subgroups “Linear 1” and “Linear 2”:
  - Linear 1: the first cue of the sequence is positioned on the top left part of the apparatus, with the chunks going from left to right from the bird's perspective. The sequence on the rows goes from top to bottom.
  - Linear 2: the first cue of the sequence is positioned on the bottom left part of the apparatus, with the chunks going from left to right from the bird’s perspective. The sequence on the rows goes from bottom to top
- “Random”: The sequence does not follow a linear pattern, but a random one, without a logical order in the position of the cues. Only the first two cues are next to each other on the same row. At the beginning of the experiments the first two cues were positioned apart, but the birds in the random groups seemed to struggle with the first additional cue. This change was made to their sequence at an early stage to make sure that the birds would understand the concept of a sequence. This did not change the effect of a linear vs. random sequence for the next steps. As with the linear group, the random group was divided into two subgroups, “Random 1” and “Random 2”:
  - Random 1: the first cue of the sequence is positioned on the top left part of the apparatus, the second on its right, while the rest of the cues follow a random order with no chunks or sub sequences. The position of the cues are independent from each other.
  - Random 2: the first cue of the sequence is positioned on the bottom right part of the apparatus, the second on its left. The cues follow the same order as the Random 1 subgroup’s sequence, but going in the opposite direction (e.g., bottom instead of top, left instead of right).

The subgroup division was done in order to increase the amount of stimulus patterns and minimise other biasing effects like a possible top row preference. Every step of the sequence was introduced one at the time (Step 1 only one light, Step 2 two lights...etc.). The criteria to reach a new step required the bird to complete two consecutive sessions with 80 % correct trials.

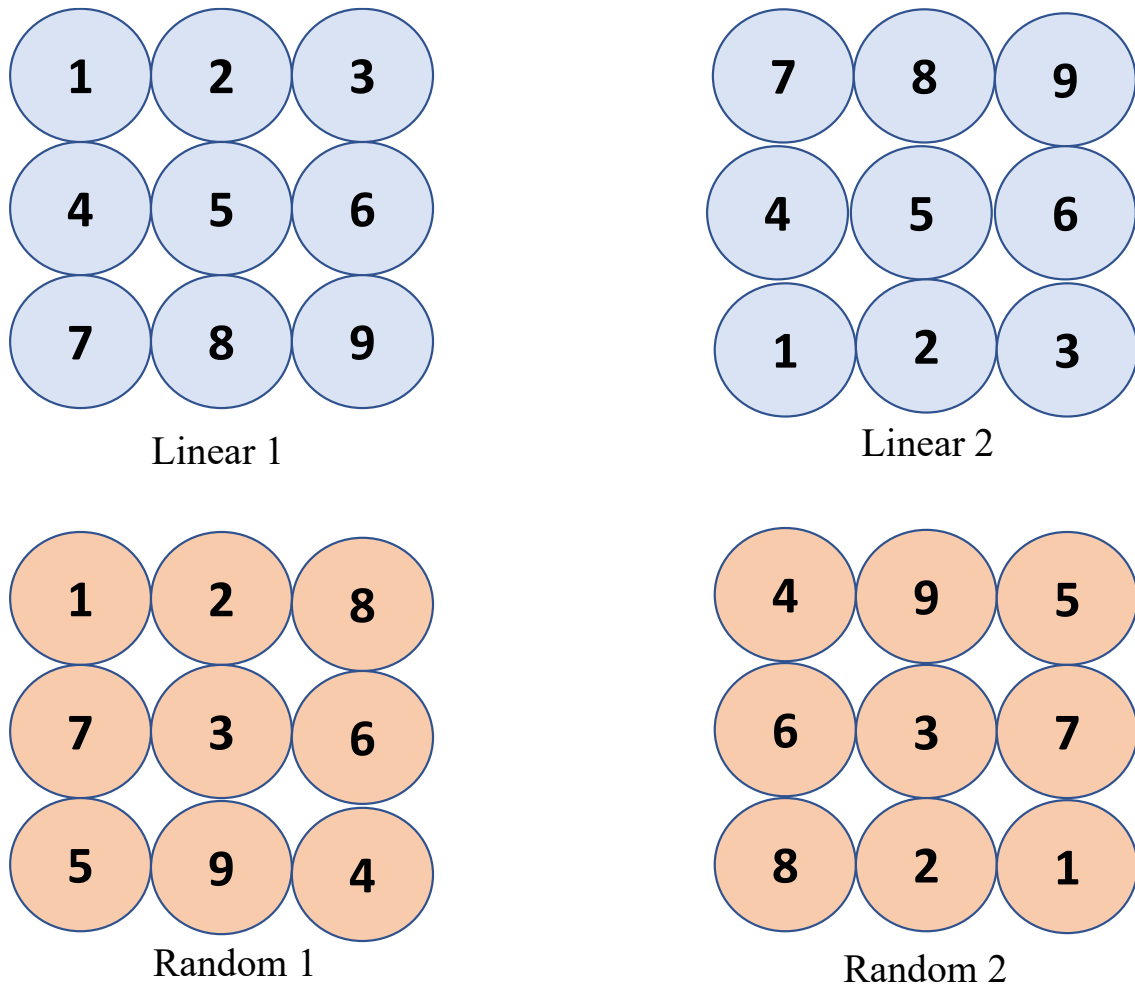


Figure 5. The different arrangement of the sequences. Linear 1 and Random 1 start from the bottom, while Linear 2 and Random 2 start from the top. The number indicate the order in which the kea were trained to touch the lights. In the linear sequences the chunks are composed by the light 123-456-789.

#### 2.4. Data collection

All the sessions were recorded by a video camera (JVC Everio R GZ-R415BE) positioned next to the apparatus. The result of every trial was noted by the experimenter by hand in a notebook.

#### 2.5. Statistical analysis

Statistical analyses were performed using the program Microsoft Excel Analysis Tool Pak. Prior to analyse the statistics, we checked to confirm the normality of the distribution of data. As the data were normally distributed, Parametric methods, Pearson correlation, t test for independent variables were used. p values were considered significant when  $<0.05$ .



### 3. Results

Nine birds completed the four training phases and reached the test phase. Three birds were able to learn the complete sequence:

- Paul and Kermit completed the linear sequence.
- Pick completed the random sequence.

One of the birds in the random sequence group, Roku, reached the 7<sup>th</sup> stage. The other five birds completed both sequences until the 3<sup>rd</sup> stage and stopped after it. For an overview of the stages reached see table 3.

*Table 3. Completed stages and number of sessions for each bird.*

<b>Name</b>	<b>Age a test time</b>	<b>Sex</b>	<b>Testing group</b>	<b>Completed stages</b>	<b>Total sessions</b>
Mali	4	Female	Linear 1	3	15
Paul	8	Male	Linear 2	9	57
Kermit	14	Male	Linear 2	9	68
Sunny	11	Female	Linear 1	3	25
Odo	3	Male	Linear 1	3	13
Roku	10	Male	Random 1	7	79
Pick	14	Male	Random 1	9	116
Fay	2	Female	Random 2	3	24
Jean-Luc	3	Male	Random 2	3	19

Results indicate that the individuals in the linear sequence group learned the task faster than individuals in the random sequence group. The difference in the relative difficulty between the

two sequences is demonstrated by the fact that if we plot the number of total sessions needed against the number of completed stages, for the linear sequence the slope of the interpolating linear equation is twice the one of the random sequence (see figure 6).

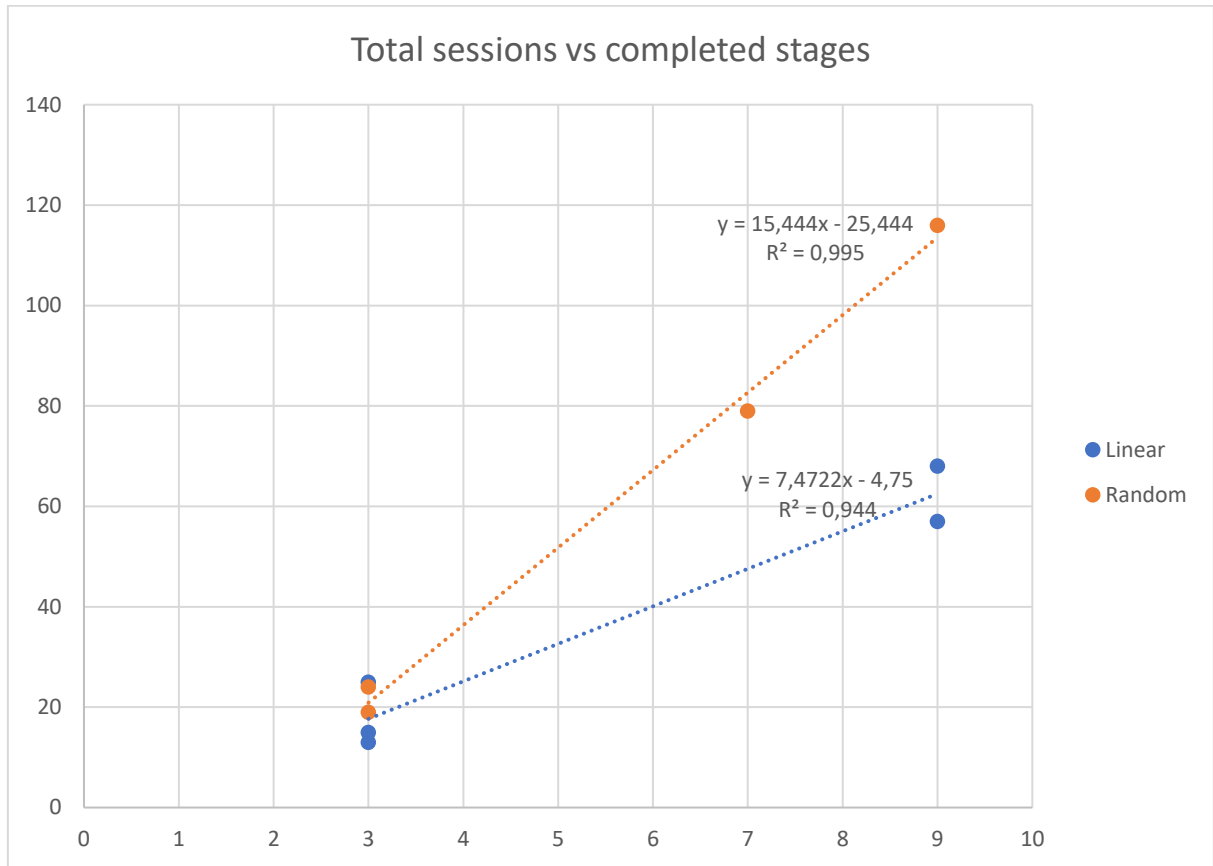


Figure 6. On the x axis, the number of stages of the test; on the y, the number of total sessions needed by every bird.

There is a statistically significant difference between the mean values of the linear and the random sequence (t test,  $p < 0.039$  one tailed) and the significance of this difference increases if we consider only the last five stages (t test,  $p < 0.004$  one tailed). For the number of sessions needed for each bird and the mean value for each stage of the test see table 4.

Table 4. Number of sessions for each stage of the test in the linear and the random sequences and their mean values

Bird	Stage 1	Stage 2	Stage 3	Stage 4	Stage 5	Stage 6	Stage 7	Stage 8	Stage 9
<b>Linear Sequence</b>									
Mali	2	5	8						
Paul	2	5	2	18	8	6	9	3	4
Kermit	2	4	3	24	10	12	9	2	2
Sunny	2	18	5						
Odo	2	5	6						
<b>Mean</b>	<b>2.0</b>	<b>7.4</b>	<b>4.8</b>	<b>21.0</b>	<b>9.0</b>	<b>9.0</b>	<b>9.0</b>	<b>2.5</b>	<b>3.0</b>
<b>St. Dev</b>	<b>0.0</b>	<b>5.9</b>	<b>2.4</b>	<b>4.2</b>	<b>1.4</b>	<b>4.2</b>	<b>0.0</b>	<b>0.7</b>	<b>1.4</b>
<b>Random Sequence</b>									
Roku	3	9	3	17	7	24	16		
Pick	2	7	9	27	13	17	9	14	19
Fay	2	7	5						
Jean-Luc	2	13	4						
<b>Mean</b>	<b>2.3</b>	<b>9.5</b>	<b>7.8</b>	<b>20.5</b>	<b>10.0</b>	<b>20.5</b>	<b>12.5</b>	<b>14.0</b>	<b>19.0</b>
<b>St. Dev</b>	<b>2.3</b>	<b>9.5</b>	<b>7.8</b>	<b>20.5</b>	<b>10.0</b>	<b>20.5</b>	<b>12.5</b>	<b>14.0</b>	<b>19.0</b>

In the linear sequence, the number of sessions for each stage of the test show that going from the 3rd light to the 4th light is the most difficult passage to learn. The test stage 4 required the highest number of sessions for both groups. There is no difference in the linear group learning speed for items 1 to 3, 4 to 6 or 7 to 9, which were all steps between buttons occurring on the same horizontal line. This is also evident if we plot the mean number of sessions for each stage, both for the birds in the linear and for those in the random sequence, as shown in figure 7.

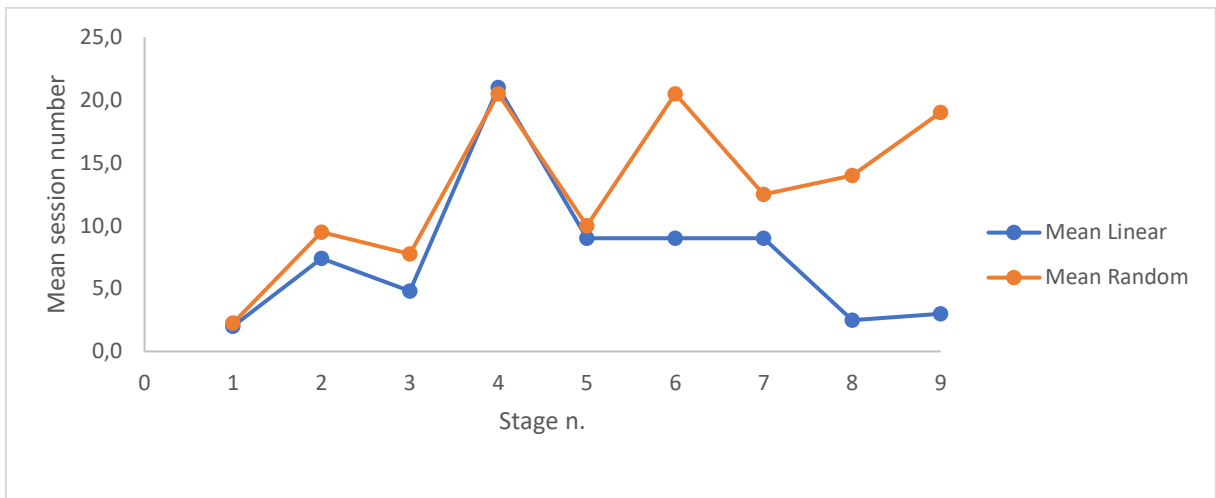


Figure 7. The number of steps that compose the sequence is represented on x axis; the mean number of sessions needed to complete every stage is represented on the y axis. It is visible how after the 4<sup>th</sup> step the number of sessions increased more in the random sequence group than the linear sequence group.

This result suggests that before the 4<sup>th</sup> stage the mean number of sessions is similar for both the linear and for the random sequence groups, while after this stage, the birds in the random sequence group encounter more difficulties than the birds in the linear group, as birds in the linear group seem to learn faster than birds from the random group after this step.

The ability to learn expressed in terms of number of completed stages and the number of total sessions is positively correlated to the birds' age (Pearsons'  $r = 0.76$ ,  $p=0.016$  and  $r = 0.80$ ,  $p=0.009$  respectively). This is also visualized in figure 8, which shows the number of completed stages plotted versus the birds' age at the time of the experiment. It should be noted that the last point (14; 9) contains the data of two birds, Pick and Kermit.

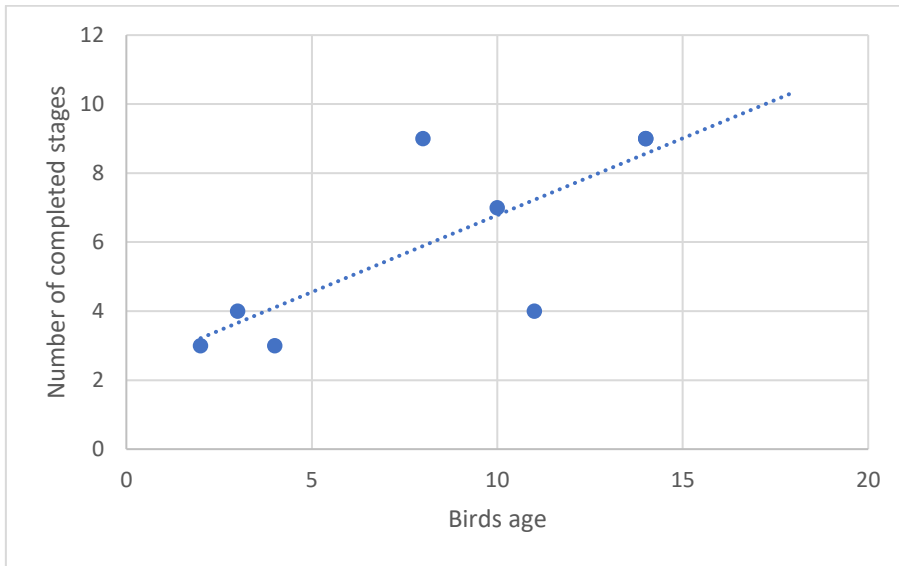


Figure 8 Number of completed stages of both groups correlated with the birds' age

Pearson's correlation among the dependent parameters (number of completed stages and number of sessions) and the independent parameters (age, sex, hand or parent raised and testing group) have been calculated and reported in table 4. Significant correlations are depicted in bold, tendencies in italics. To note that all birds that completed all the nine stages of the test were males.

Table 5. Pearson's correlation between the depended and independent parameters

<b>Correlation</b>	Age at test time	Hand/Parent raised	Sex	Testing group	Completed stages
Completed stages	<b>0.764</b>	<i>0.394</i>	<b>0.619</b>	0.018	1
Total sessions	<b>0.803</b>	<i>0.490</i>	<b>0.520</b>	<i>0.351</i>	<b>0.876</b>

If the number of trials in every session is cumulated, as previously done for the sessions, while separating the successful trials from the unsuccessful trials before reaching the criteria for every stage, two interesting plots are obtained. These are reported in figures 9 and 10.

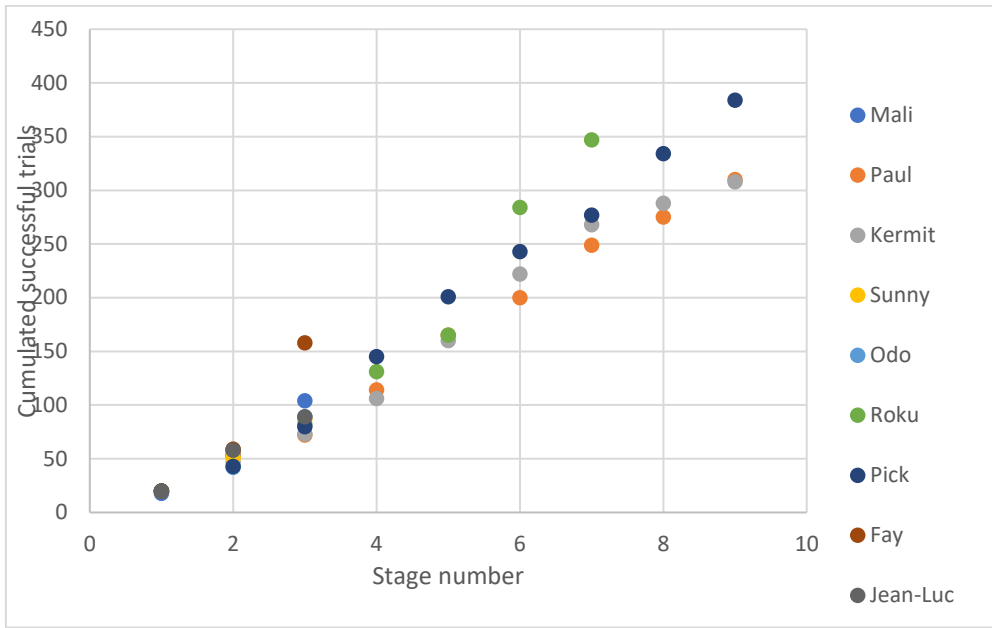


Figure 9. Cumulated number of successful trials for every bird for every stage before reaching the criteria.

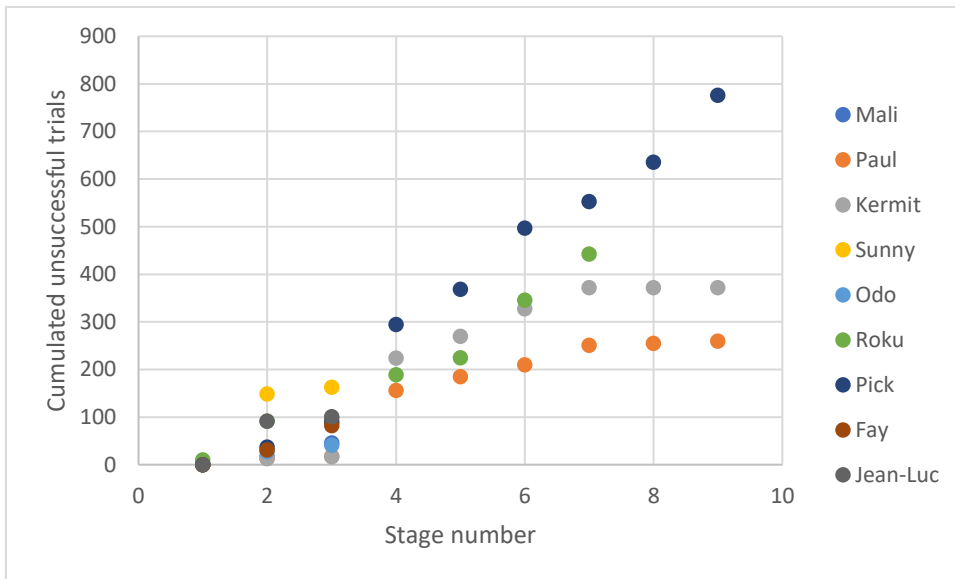


Figure 10 Cumulated number of unsuccessful trials for every bird for every stage before reaching the criteria.

It is worth noting that, while the cumulated successful trials seem to follow the cumulated sessions, the graphical representation of the cumulated unsuccessful trials clearly shows that the two birds involved in the linear sequence group after the stage 6 do not make mistakes anymore.

Another way of representing the trends of the experiment for each bird is shown in figure 11, where the unsuccessful trials have been transformed in negative numbers, showing the extent of the effort made by each subject in trying to learn the assigned task. From this figure it can be seen again that stage 4 presented the highest number of unsuccessful trials for both the sequence patterns.

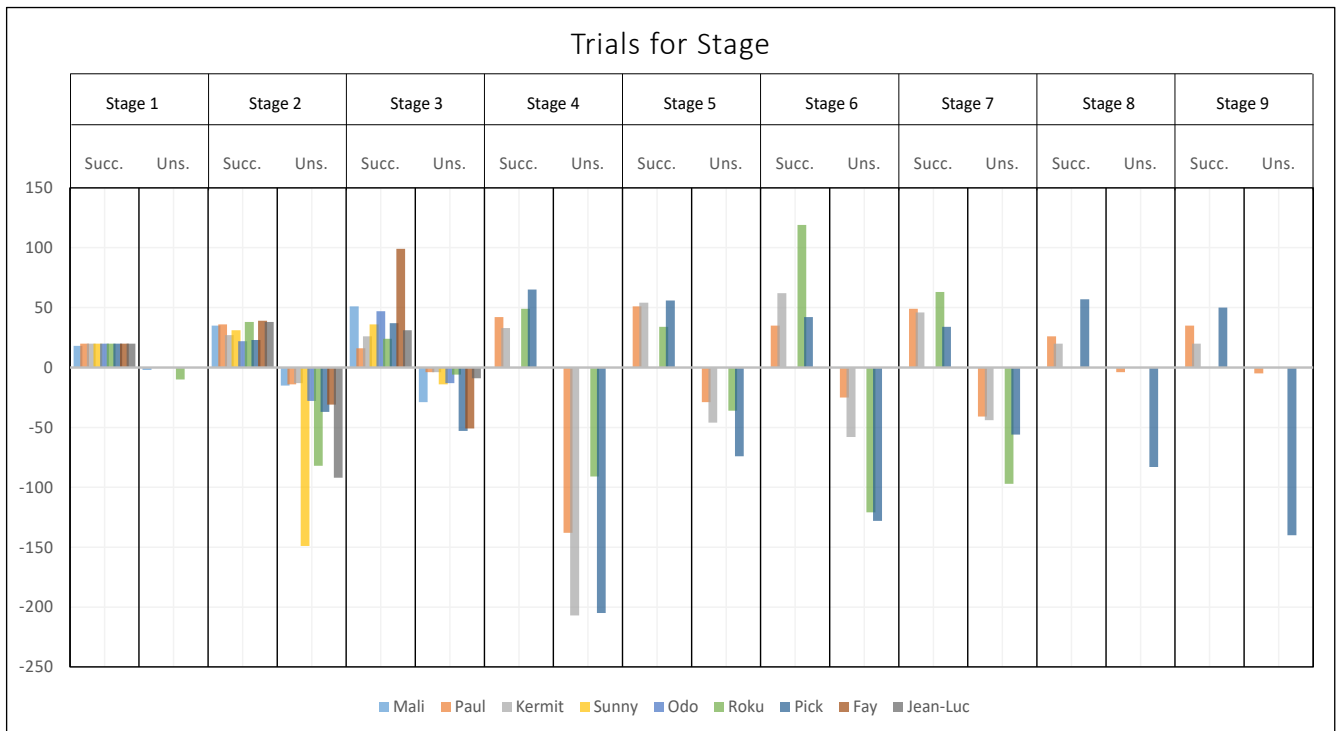


Figure 11. Number of successful (Suc.) and unsuccessful (Uns) trials in each stage depicted as positive and negative numbers. The stage number is also indicated. Is visible how the highest number of unsuccessful trials in in stage 4.

In table 6, the mean number of trials for each stage is reported, separately for successful and unsuccessful. The difference between Linear and Random was statistically significant (T test,  $p=0.036$  one tailed) for the successful trials, and close to the significance for the unsuccessful trials ( $p=0.058$ , one tailed).

*Table 6. Mean number of trials for each stage separated for successful and unsuccessful.*

Stage n.	Successful Trials		Unsuccessful trials	
	Mean Linear	Mean Random	Mean Linear	Mean Random
Stage 1	19.6	20	0.4	2.5
Stage 2	30.2	34.5	43.8	60.5
Stage 3	35.2	47.75	12.8	29.75
Stage 4	37.5	57	172.5	148
Stage 5	52.5	45	37.5	55
Stage 6	48.5	80.5	41.5	124.5
Stage 7	47.5	48.5	42.5	76.5
Stage 8	23	57	2	83
Stage 9	27.5	50	2.5	140



#### 4. Discussion

The present experiment aimed to test whether kea parrots are able to learn a complex sequence consisting of 9 separate actions, learned in a step wise fashion. Three birds out of nine, Paul, Kermit and Pick, were able to learn the complete respective sequences. Specifically, a sequence of steps without a difference in the type of action required. The results revealed some interesting findings. First, the birds in the linear group learned the sequence faster than those in the random group. This evidence is especially important because it reveals that the arrangement of the sequence might play a role in the learning process, influencing how fast learning occurs as well as the mechanism used by the kea to learn the sequences. The linear sequence contains a chunking pattern which is repeated three times (123-456-789); this suggests that the birds might use a chunking mechanism to learn the sequence, and that the repetitive pattern affected the learning speed and modality. This is in line with the fact that birds have already been observed to be sensitive to patterns in a sequence (Froehlich et al., 2004; Garlick et al., 2017). Pick, who completed the random sequence, took 116 sessions to learn all the 9 steps, a higher number of sessions than either Paul or Kermit, who completed the linear sequence with 57 and 68 sessions respectively. Roku took 79 sessions and but only reached stage 7 of the random sequence. For all the birds, the 4<sup>th</sup> step was the hardest to learn. The first 2 steps are the same in the two sequences, in the random sequence the third one is different but still adjacent to the previous step, while the 4<sup>th</sup> represents the first step that for both groups was more distant to the previous light and required the bird to read the other side of the apparatus. This fact might show that another factor that might have helped the birds in the linear to group to learn the sequence easier is that the positions of the majority of the cues are adjacent, while in the random group after the third step the cues are always far from each other. The probability of touching the right cues at the beginning was easier, and the kea might have used a trial-and-error strategy at least for the beginning of the sequence. This would be consistent with the results obtained by Garlick et al in their work on serial pattern learning in pigeons, where it was observed that at an easy level of cues, the pigeons used associative learning rather than serial-pattern learning, but later used chunking mechanism to learn more complex sequences (Garlick et al., 2017). What could have

happened is that the birds that succeeded in learning the whole sequence used a chunking mechanism after the 4<sup>th</sup> step, while the others kept on using associative learning with trial and errors, and due to the increased distance from the steps they were not able to learn the following steps. It could also be that if the sequence were made of only adjacent steps, both in the random and linear sequence, the parrots could have learned the positions of the cues easily, while only using a trial-and-error mechanism, but we would not be able to discriminate if the arrangement of the sequence or the spatial ordinality of the cues had played a role in the learning mechanism of the kea. They might still learn the sequence, and might even learn it faster, but it would be difficult to distinguish if only mechanisms of simple associations are playing a role in this case.

In most of the studies on sequential learning, especially in humans, reaction time is used as a parameter to assess proficiency in tests. But in the case of this study, the time between touching one light and the following was highly dependent on the immediate interest and subjective temperament and mood of the bird. This phenomenon has already been observed in other works with parrots: the most explicit example is with the parrot Alex, with whom it was observed that the reaction time depended on the immediate interest in the task when learning ordinality and categorizations of quantity (Pepperberg, 2002). Anecdotal observations during the experiment show how parrots that completed the sequence, such as Paul and Roku, took more time between one button and another than other birds, such as Odo, who touched the lights extremely fast but never reached stage 4 of the test. Thus, fast reaction time in this experiment cannot be used as a proficiency parameter because taking more time could mean paying more attention to the lights and remembering how the steps were shown before the Plexiglas was removed. This observation might also indicate that the birds that touched the lights very fast, making many mistakes without ever reaching stage 4 of the test, could have been looking for a fast way to get a reward, casually touching the lights. Consequently, it was easier to reach for lights closer to the third button than it was to reach the 4<sup>th</sup> button, which required the parrots to move to the other side or the apparatus (left to right or right to left) in case of both linear and random sequences.

Error rate might instead provide a measure of difficulty (Pepperberg, 2006). If we look at the cumulated number of unsuccessful trials of Paul and Kermit, who were in the linear group (Figure 10), it is very interesting to note how after stage 7 the number of mistakes seem to drop

rather than increase. This is quite different in respect to the cumulative mistakes made by Pick (random group), which remain constant during all the stages of the test. It is useful to highlight this difference, which shows how much the last three steps of the linear sequence became easy for the birds who completed the test, to the point of making almost no more mistakes. Furthermore, the number of trials completed while moving from step 8 to 9 were notably smaller than those for other steps. This strengthens the hypothesis that the birds learned how the sequence is structured with the presence of chunks. This is further supported by the presence of some anticipation during the last two steps of the sequence for Paul and Kermit. During stage 8, both birds tried to touch the 9<sup>th</sup> light after having completed the sequence until step 8, before the following stage was shown by the experimenter. This might demonstrate how the birds already imagined what the next step would be, without the need for a demonstration or any trial-and-error mechanism.

Another phenomenon observed with all the subjects during the test was that they would sometimes start the sequence, skip the buttons in the middle and jump directly to the last one of that stage they were in. If the parrots touched the button at the end of the sequence avoiding touching the ones in the middle, it might indicate that they wanted to reach the end of the sequence, because they understood when the reward would come. Skip errors were also the most common in the study on sequential learning in gorillas and chimpanzees, independent from their position (Kawai & Matsuzawa, 2001; Ross, 2009). A further example, in several experiments on simultaneous chaining with cotton-top tamarins (*Saguinus oedipus*) and pigeons (*Columba livia*) by Locurto and colleagues, it has been observed that if the subjects would choose a step of the sequence that followed in the chain rather than one that was closer to the end of the sequence and thus closer to the reward, that step was presumably of higher associative strength. Therefore this finding suggests that the links between elements in the chain were not solely dependent on associative strength, but also reflected other forms of association, such as stimulus–stimulus or stimulus–response learning (Locurto et al., 2010, 2013, 2015). In fact, most chaining models such as this one encounter difficulties in dealing with repeated items where responses are represented by the same cue, and this model would also have a higher probability of presenting erroneous responses, which could lead to a series of subsequent errors (Chen & ten Cate, 2015).

Nevertheless, trial-and-error learning is necessary to master lists composed of arbitrary items (Terrace, 2005). This is especially important in our case because of the absence of any difference in the kind of items that compose the sequence, which surely plays an important role. But if trial and error were the only mechanisms applied by the birds in this experiment, the different sequences would be of equal difficulty (Terrace, 2005). If they did not pay any attention to the sequences presented before the Plexiglas was removed, the chunking mechanism would probably not have taken place. This is also particularly evident in the difference number of trials taken by Paul and Kermit while learning stage 4 and stage 7. The distance between the lights 3 and 4 and the lights 6 and 7 in the linear sequence are the same, and they are also in the same position, but one is above the other (see fig.5). Our results show that the 4<sup>th</sup> step was the hardest to learn, as it took 18 sessions for Paul and 24 for Kermit. However, for the 7<sup>th</sup> step both the birds took 9 sessions to complete the stage, a smaller number of sessions. This is an important result because it shows that the birds learned how the big “step” works, after struggling so much the first time, and that they applied the chunking mechanism. It is interesting to compare this result with the ones from the studies on a sequence of 9 steps in chimpanzees and gorillas, where the subjects took more time and had longest response time for the first number of the sequence, and shorter times for all the other numbers without differences from using spatial cues (Inoue & Matsuzawa, 2009; Kawai & Matsuzawa, 2001; Ross, 2009). A fundamental difference between the present study and the one on non-human primates is that, even if they all explored a sequence of 9 items, when the chimps or the gorilla touched the right cue it would disappear from the touchscreen, and it would become easier to select the next cue. In our study with the kea the cue are present all the time on the apparatus, they don't disappear, and this represents an increased level of difficulty, giving more opportunity for “background errors” (Ross, 2009). This features more closely to a simultaneous chain paradigm, (SCP) , where instead of having the items of a sequence presented in a successive order with the choices isolated from each other, the choices are presented all together “simultaneously”, with the possibility to make mistakes at any point of the sequence (Terrace, 2005), but with a unique reward at the end of the whole sequence.

All these results support the hypothesis that the arrangement of the sequence significantly influences the kea's learning speed. Furthermore, we can assume that the kea rely on chunking mechanisms to learn the sequence, due to the fact that the birds in the linear group learned the sequence faster than the ones in the random group. There was a difference in the learning speed, which increased after learning the first fixed chunk pattern in the linear sequence. This shows how the main learning mechanism is use of chunking, probably more than spatial ordinality. This does not exclude that elements of both these mechanisms, and others such as simple trial and error, might play a role in the whole learning process. Intelligent behaviour is greater than the sum of discrete conditioned responses (Terrace, 2005). The mechanisms of learning might vary from an individual to another and define the reason why some of the birds could not go beyond the 4<sup>th</sup> step. After completing first three steps, Jean-Luc, Odo, Fay, Mali and Sunny tried to reach stage 4 through a large number of trials, but they were never able to complete the criteria to pass to the next stage. After months of testing in the 4<sup>th</sup> step these birds lost motivation and interest in the test, due to the fact that they had been rewarded very rarely. Their choices, after a while, started to be more casual and seemed more likely to be the result of trial and error mechanisms, making mistakes even during the part of the sequences they had already learned and demonstrated correctly.

The case of Roku seems more complicated, as he reached stage 7 and then he lost motivation in the same way as the birds that stopped at stage 4. Conditions such as mating season and group dynamics during the stage time might have influenced his loss of motivation. Another factor to be considered is the age of the kea. The oldest birds, with the exception of Sunny, solved the task, but this might also be linked to experience and general training time. This result differs from the chimpanzees study, where one of the goals of the study was to explore age difference in sequential learning, and between 6 subjects that solved the task no age difference was found (Inoue & Matsuzawa, 2009).

One of the weakness of this study is the small number of subjects involved and the fact that only three birds managed to learn complete sequences. This factor suggests that these results represent only a preliminary example and a larger number of subjects might lead to a better understanding of this phenomenon. It would be interesting to see if future studies on the topic, with different patterns and a greater number of subjects, could confirm our results. In general,

this study shows that kea parrots are able to learn a complex sequence, as has been observed in other animals including pigeons, rats, non-human primates and humans themselves (Conway & Christiansen, 2001; Garlick et al., 2017; Muller & Fountain, 2010; Spiegel & McLaren, 2006).

As discussed in the introduction, sequential learning plays a role in predicting seriality of events on the animal's environment and it is essential for survival. It is applied by animals in their ecological context in their everyday behaviour. A good example of how sequential learning is integrated in the action of a normal behaviour is given by Locurto: "*Consider an animal foraging in its habitat: the route to food may be uncertain. It is only after finding food that the prior sequence of turns and pathways becomes relevant. It would be extraordinarily disadvantageous if it were only at the moment of finding food that the animal began to wonder: 'How did I get here?'*" The storing of, in this case, a spatial sequence had to occur before it could be determined that the sequence was useful. Something similar must be true for predator avoidance." (Locurto et al., 2013). Kea are extractive foragers (O'Hara et al., 2015), generalists that feed on many different plant species and perform seasonal movements based on the availability of food (Brejaart, 1988). This kind of dynamic could easily involve mechanisms of sequential learning to help orientation and to save energy while looking for food resources. The environment in which these animals live is full of information, but being able to identify and recognise regularities might be essential to survival and for making a sense of the complex environment. For example, a sequence of items composed of foraging patches can generate a stable sequence of visits which can help to reduce the times a patch is visited multiple times, with the consequence of saving precious time (Pfuhl & Biegler, 2012). These kinds of mechanisms could relate to navigation, communication, or behavioural sequence to recognize connected (sibling or same species) individuals. Sequences can be found even in behaviours such as play, which in kea is composed by temporal sequences, and repeated actions by mutual initiative (Bond & Diamond, 2004). Furthermore, on a more generalized level, sequential learning might represent a way to become closer to repeated structures that are meant to be more familiar, such as siblings, or species-specific cues; this would favour the imprinting on siblings in a natural environment (Santolin et al., 2016). For these reasons, this study represents an important first step into a fruitful topic of research in kea.

## 5. Summary (EN)

Sequential learning is defined as the ability to create associations of items into a sequence and putting them into an ordered series. The ability of sequencing information is fundamental in humans and animals to solve a variety of tasks and represents one of the most prevalent form of learning. Sequential learning is essential to predict seriality in events in the animal's environment and therefore essential for survival. Different underlying mechanisms can be involved in sequential learning. "chunking", which is the act of dividing and segmenting a sequence into smaller blocks (chunks) that have a strong association with one another, but weaker associations with other chunks. Spatial ordinality represent the mechanism of encoding the positions of the items inside a sequence, understanding their relative position to one another into space. In order to learn more about sequential learning, the present study tested the ability of kea (*Nestor notabilis*) to learn a complex sequence of 9 steps without a difference in the type of action required. Nine birds were trained to peck at visual stimuli before being tested on a predetermined "linear" or "random" sequence. Three birds out of nine were able to learn the sequence, and the results shows that the arrangement of the sequence might play a role in the learning process, specifically the birds seem to use a chunking mechanism as driven for sequential learning. This result is in line with previous studies on sequential learning in birds.

## 6. Zusammenfassung (DE)

Sequentielles Lernen ist definiert als die Fähigkeit, Assoziationen von Elementen in eine Sequenz zu bringen und sie in eine geordnete Reihe zu stellen. Die Fähigkeit, Informationen in eine Reihenfolge zu bringen, ist bei Menschen und Tieren grundlegend, um eine Vielzahl von Aufgaben zu lösen, und stellt eine der am weitesten verbreiteten Formen des Lernens dar. Sequentielles Lernen ist essentiell für die Vorhersage der Serialität von Ereignissen in der Umwelt des Tieres und somit überlebenswichtig. Am sequentiellen Lernen können verschiedene zugrundeliegende Mechanismen beteiligt sein. "Chunking", d.h. die Aufteilung und Segmentierung einer Sequenz in kleinere Blöcke (Chunks), die eine starke Assoziation zueinander, aber schwächere Assoziationen zu anderen Chunks haben. Räumliche Ordinalität stellt den Mechanismus der Kodierung der Positionen der Elemente innerhalb einer Sequenz dar, wobei ihre relative Position zueinander im Raum verstanden wird. Um mehr über sequenzielles Lernen zu erfahren, wurde in der vorliegenden Studie die Fähigkeit von Keas (*Nestor notabilis*) getestet, eine komplexe Sequenz von 9 Schritten zu erlernen, ohne dass ein Unterschied in der Art der erforderlichen Aktion besteht. Neun Vögel wurden darauf trainiert, auf visuelle Reize zu picken, bevor sie auf eine vorgegebene "lineare" oder "zufällige" Sequenz getestet wurden. Drei von neun Vögeln waren in der Lage, die Sequenz zu erlernen, und die Ergebnisse zeigen, dass die Anordnung der Sequenz eine Rolle im Lernprozess spielen könnte, insbesondere scheinen die Vögel einen Chunking-Mechanismus als Antrieb für das sequenzielle Lernen zu verwenden. Dieses Ergebnis steht im Einklang mit früheren Studien zum sequenziellen Lernen bei Vögeln.



## 7. References

- Auersperg, A. M. I., von Bayern, A. M. P., Gajdon, G. K., Huber, L., & Kacelnik, A. (2011). Flexibility in problem solving and tool use of kea and new caledonian crows in a multi access box paradigm. *PLoS ONE*, 6(6). <https://doi.org/10.1371/journal.pone.0020231>
- Bond, A. B., & Diamond, J. (2004). *DigitalCommons @ University of Nebraska - Lincoln Social Play in Kaka ( Nestor meridionalis ) with Comparisons to Social Play in Kaka ( Nestor meridionalis ) with Comparisons to Kea ( Nestor notabilis )*.
- Brejaart, R. (1988). *Diet and Feeding Behaviour of the Kea (Nestor notabilis)*. 87.
- Capaldi, E. J., & Molina, P. (1979). Element discriminability as a determinant of serial-pattern learning. *Animal Learning & Behavior*, 7(3), 318–322. <https://doi.org/10.3758/BF03209676>
- Chen, J., & ten Cate, C. (2015). Zebra finches can use positional and transitional cues to distinguish vocal element strings. *Behavioural Processes*, 117, 29–34. <https://doi.org/10.1016/j.beproc.2014.09.004>
- Chen, S., Swartz, K. B., & Terrace, H. S. (1997). Knowledge of the Ordinal Position of List Items in Rhesus Monkeys. *Psychological Science*, 8(2), 80–86. <https://doi.org/10.1111/j.1467-9280.1997.tb00687.x>
- Christiansen, M. H. (2019). Implicit Statistical Learning: A Tale of Two Literatures. *Topics in Cognitive Science*, 11(3), 468–481. <https://doi.org/10.1111/tops.12332>
- Christiansen, M. H., & Chater, N. (2016). The Now-or-Never bottleneck: A fundamental constraint on language. *The Behavioral and Brain Sciences*, 39, e62. <https://doi.org/10.1017/S0140525X1500031X>
- Clegg, B. A., DiGirolamo, G. J., & Keele, S. W. (1998). Sequence learning. *Trends in Cognitive Sciences*, 2(8), 275–281. [https://doi.org/10.1016/S1364-6613\(98\)01202-9](https://doi.org/10.1016/S1364-6613(98)01202-9)
- Conway, C. M. (2012). Sequential Learning. In N. M. Seel (Ed.), *Encyclopedia of the Sciences*

*of Learning* (pp. 3047–3050). Springer US. [https://doi.org/10.1007/978-1-4419-1428-6\\_72](https://doi.org/10.1007/978-1-4419-1428-6_72)

Conway, C. M., & Christiansen, M. H. (2001). Sequential learning in non-human primates. *Trends in Cognitive Sciences*, 5(12), 539–546. [https://doi.org/10.1016/S1364-6613\(00\)01800-3](https://doi.org/10.1016/S1364-6613(00)01800-3)

Conway, C. M., Karpicke, J., & Pisoni, D. B. (2007). Contribution of Implicit Sequence Learning to Spoken Language Processing: Some Preliminary Findings With Hearing Adults. *Journal of Deaf Studies and Deaf Education*, 12(3), 317–334. <https://doi.org/10.1093/deafed/enm019>

Dallal, N. L., & Meck, W. H. (1990). Hierarchical structures: chunking by food type facilitates spatial memory. *Journal of Experimental Psychology. Animal Behavior Processes*, 16(1), 69–84. <https://doi.org/10.1037/0097-7403.16.1.69>

Daltrozzo, J., & Conway, C. M. (2014). Neurocognitive mechanisms of statistical-sequential learning: what do event-related potentials tell us? *Frontiers in Human Neuroscience*, 8, 1–22. <https://doi.org/10.3389/fnhum.2014.00437>

Diamond, J., & Bond, A. B. (1999). *Kea, bird of paradox. The evolution and behavior of a New Zealand parrot*. University of California Press.

Drucker, C. B., Baghdoyan, T., & Brannon, E. M. (2016). Implicit sequence learning in ring-tailed lemurs ( *Lemur catta* ). *Journal of the Experimental Analysis of Behavior*, 105(1), 123–132. <https://doi.org/10.1002/jeab.180>

Endress, A. D., Carden, S., Versace, E., & Hauser, M. D. (2010). The apes' edge: Positional learning in chimpanzees and humans. *Animal Cognition*, 13(3), 483–495. <https://doi.org/10.1007/s10071-009-0299-8>

Fonollosa, J., Neftci, E., & Rabinovich, M. (2015). Learning of Chunking Sequences in Cognition and Behavior. *PLOS Computational Biology*, 11(11), e1004592. <https://doi.org/10.1371/journal.pcbi.1004592>

Fountain, S. B. (2008). Pattern Structure and Rule Induction in Sequential Learning.

*Comparative Cognition & Behavior Reviews*, 3, 66–85.  
<https://doi.org/10.3819/ccbr.2008.30004>

Fountain, S. B., Evensen, J. C., & Hulse, S. H. (1983). Formal structure and pattern length in serial pattern learning by rats. *Animal Learning & Behavior*, 11(2), 186–192.  
<https://doi.org/10.3758/BF03199647>

Fountain, S. B., & Hulse, S. H. (1981). Extrapolation of serial stimulus patterns by rats. *Animal Learning & Behavior*, 9(3), 381–384. <https://doi.org/10.3758/BF03197847>

Fountain, S. B., & Rowan, J. D. (1995). Sensitivity to violations of “run” and “trill” structures in rat serial-pattern learning. In *Journal of Experimental Psychology: Animal Behavior Processes* (Vol. 21, Issue 1, pp. 78–81). American Psychological Association.  
<https://doi.org/10.1037/0097-7403.21.1.78>

Fountain, S., Bunsey, M., Danks, J., & Mcbeath, M. (2002). *Animal Cognition and Sequential Behavior: Behavioral, Biological, and Computational Perspectives*.  
<https://doi.org/10.1007/978-1-4615-0821-2>

Froehlich, A. L., Herbranson, W. T., Loper, J. D., Wood, D. M., & Shimp, C. P. (2004). Anticipating by Pigeons Depends on Local Statistical Information in a Serial Response Time Task. *Journal of Experimental Psychology: General*, 133(1), 31–45.  
<https://doi.org/10.1037/0096-3445.133.1.31>

Garlick, D., Fountain, S. B., & Blaisdell, A. (2017). Serial Pattern Learning in Pigeons: Rule-Based or Associative? *Journal of Experimental Psychology: Animal Learning and Cognition*, 43(1), 30–47.

Gobet, F., Lane, P. C. R., Croker, S., Cheng, P. C., Jones, G., Oliver, I., & Pine, J. M. (2001). Chunking mechanisms in human learning. In *Trends in Cognitive Sciences* (Vol. 5, Issue 6, pp. 236–243). [https://doi.org/10.1016/S1364-6613\(00\)01662-4](https://doi.org/10.1016/S1364-6613(00)01662-4)

Haggbloom, S. J. (1985). Serial learning and transfer in rats: Effects of changes in stimulus-stimulus associations, pattern structure, and serial position information. *Animal Learning & Behavior*, 13(4), 370–374. <https://doi.org/10.3758/BF03208012>

- Huber, L., & Gajdon, G. K. (2006). Technical intelligence in animals: The kea model. *Animal Cognition*, 9(4), 295–305. <https://doi.org/10.1007/s10071-006-0033-8>
- Huber, L., Rechberger, S., & Taborsky, M. (2001). Social learning affects object exploration and manipulation in keas, *Nestor notabilis*. *Animal Behaviour*, 62(5), 945–954. <https://doi.org/10.1006/anbe.2001.1822>
- Hulse, S. H., & Campbell, C. E. (1975). “Thinking ahead” in rat discrimination learning. *Animal Learning & Behavior*, 3(4), 305–311. <https://doi.org/10.3758/BF03213451>
- Hulse, S. H., & Dorsky, N. P. (1977). Structural complexity as a determinant of serial pattern learning. *Learning and Motivation*, 8(4), 488–506. [https://doi.org/10.1016/0023-9690\(77\)90047-9](https://doi.org/10.1016/0023-9690(77)90047-9)
- Hulse, S. H., & Dorsky, N. P. (1979). Serial pattern learning by rats: Transfer of a formally defined stimulus relationship and the significance of nonreinforcement. *Animal Learning & Behavior*, 7(2), 211–220. <https://doi.org/10.3758/BF03209273>
- Hulse, S. H., & O’Leary, D. K. (1982). Serial pattern learning: Teaching an alphabet to rats. *Journal of Experimental Psychology: Animal Behavior Processes*, 8(3), 260–273. <https://doi.org/10.1037/0097-7403.8.3.260>
- Inoue, S., & Matsuzawa, T. (2009). Acquisition and memory of sequence order in young and adult chimpanzees (*Pan troglodytes*). *Animal Cognition*, 12(1 SUPPL), 59–69. <https://doi.org/10.1007/s10071-009-0274-4>
- Isbilen, E. S., McCauley, S. M., Kidd, E., & Christiansen, M. H. (2020). Statistically Induced Chunking Recall: A Memory-Based Approach to Statistical Learning. *Cognitive Science*, 44(7). <https://doi.org/10.1111/cogs.12848>
- Kawai, N., & Matsuzawa, T. (2001). “Magical number 5” in a chimpanzee. *Behavioral and Brain Sciences*, 24(1), 127–128. <https://doi.org/10.1017/S0140525X0135392X>
- Kelly, M. H., & Martin, S. (1994). Domain-general abilities applied to domain-specific tasks: Sensitivity to probabilities in perception, cognition, and language. *Lingua*, 92(C), 105–140. [https://doi.org/10.1016/0024-3841\(94\)90339-5](https://doi.org/10.1016/0024-3841(94)90339-5)

- Lashley, K. (1951). The problem of serial order in behavior. In *Cerebral mechanisms in behavior* (Issue 7, pp. 112–147). [http://books.google.com/books?hl=en&lr=&id=AqnzXFRU\\_BoC&oi=fnd&pg=PA118&dq=The+Problem+of+Serial+Order+in+Behavior&ots=hPyCJTnlTq&sig=nuMFcEmlbxnE5a9fH72casFdhyk](http://books.google.com/books?hl=en&lr=&id=AqnzXFRU_BoC&oi=fnd&pg=PA118&dq=The+Problem+of+Serial+Order+in+Behavior&ots=hPyCJTnlTq&sig=nuMFcEmlbxnE5a9fH72casFdhyk)
- Locurto, C., Dillon, L., Collins, M., Conway, M., & Cunningham, K. (2013). Implicit chaining in cotton-top tamarins (*Saguinus oedipus*) with elements equated for probability of reinforcement. *Animal Cognition*, *16*(4), 611–625. <https://doi.org/10.1007/s10071-013-0598-y>
- Locurto, C., Fox, M., & Mazzella, A. (2015). Implicit learning in cotton-top tamarins (*Saguinus oedipus*) and pigeons (*Columba livia*). *Learning and Behavior*, *43*(2), 129–142. <https://doi.org/10.3758/s13420-015-0167-0>
- Locurto, C., Gagne, M., & Nutile, L. (2010). Characteristics of implicit chaining in cotton-top tamarins (*Saguinus oedipus*). *Animal Cognition*, *13*(4), 617–629. <https://doi.org/10.1007/s10071-010-0312-2>
- McCauley, S. M., & Christiansen, M. H. (2019). Language learning as language use: A cross-linguistic model of child language development. *Psychological Review*, *126*(1), 1–51. <https://doi.org/10.1037/rev0000126>
- Milne, A. E., Wilson, B., & Christiansen, M. H. (2018). Structured sequence learning across sensory modalities in humans and nonhuman primates. In *Current Opinion in Behavioral Sciences* (Vol. 21, pp. 39–48). Elsevier Ltd. <https://doi.org/10.1016/j.cobeha.2017.11.016>
- Muller, M. D., & Fountain, S. B. (2010). Concurrent cognitive processes in rat serial pattern learning: Item memory, serial position, and pattern structure. *Learning and Motivation*, *41*(4), 252–272. <https://doi.org/10.1016/j.lmot.2010.08.003>
- Nissen, M. J., & Bullemer, P. (1987). Attentional requirements of learning: Evidence from performance measures. *Cognitive Psychology*, *19*(1), 1–32. [https://doi.org/https://doi.org/10.1016/0010-0285\(87\)90002-8](https://doi.org/https://doi.org/10.1016/0010-0285(87)90002-8)
- O’Hara, M., Huber, L., & Gajdon, G. K. (2015). The advantage of objects over images in

- discrimination and reversal learning by kea, *Nestor notabilis*. *Animal Behaviour*, *101*(March), 51–60. <https://doi.org/10.1016/j.anbehav.2014.12.022>
- Pepperberg, I. M. (2002). Cognitive and communicative abilities of grey parrots. *Current Directions in Psychological Science*, *11*(3), 83–87. <https://doi.org/10.1111/1467-8721.00174>
- Pepperberg, I. M. (2006). Ordinality and inferential abilities of a grey parrot (*Psittacus erithacus*). *Journal of Comparative Psychology*, *120*(3), 205–216. <https://doi.org/10.1037/0735-7036.120.3.205>
- Pfuhl, G., & Biegler, R. (2012). Ordinality and novel sequence learning in jackdaws. *Animal Cognition*, *15*(5), 833–849. <https://doi.org/10.1007/s10071-012-0509-7>
- Potrich, D., Rugani, R., Sovrano, V. A., Regolin, L., & Vallortigara, G. (2019). Use of numerical and spatial information in ordinal counting by zebrafish. *Scientific Reports*, *9*(1), 1–10. <https://doi.org/10.1038/s41598-019-54740-8>
- Restle, F., & Brown, E. R. (1970). Serial pattern learning: Pratraining of runs and trills. *Journal of Experimental Psychology*, *83*(1 PART 1), 120–125. <https://doi.org/10.1037/h0028530>
- Restle, F., & Burnside, B. L. (1972). Tracking of serial patterns. *Journal of Experimental Psychology*, *95*(2), 299–307. <https://doi.org/10.1037/h0033619>
- Roitblat, H. L., Pologe, B., & Scopatz, R. A. (1983). The representation of items in serial position. *Animal Learning & Behavior*, *11*(4), 489–498. <https://doi.org/10.3758/BF03199806>
- Ross, S. R. (2009). Sequential list-learning by an adolescent lowland gorilla ( *Gorilla gorilla gorilla* ) using an infrared touchframe apparatus. *Interaction Studies: Social Behaviour and Communication in Biological and Artificial Systems**Interaction Studies*, *10*(2), 115–129. <https://doi.org/10.1075/is.10.2.02ros>
- Sakai, K., Kitaguchi, K., & Hikosaka, O. (2003). Chunking during human visuomotor sequence learning. *Experimental Brain Research*, *152*(2), 229–242. <https://doi.org/10.1007/s00221-003-1548-8>

- Santolin, C., Rosa-Salva, O., Regolin, L., & Vallortigara, G. (2016). Generalization of visual regularities in newly hatched chicks (*Gallus gallus*). *Animal Cognition*, *19*(5), 1007–1017. <https://doi.org/10.1007/s10071-016-1005-2>
- Scarf, D., & Colombo, M. (2011). Knowledge of the Ordinal Position of List Items in Pigeons. *Journal of Experimental Psychology: Animal Behavior Processes*, *37*(4), 483–487. <https://doi.org/10.1037/a0023695>
- Schwarb, H., & Schumacher, E. H. (2012). Generalized lessons about sequence learning from the study of the serial reaction time task. *Advances in Cognitive Psychology*, *8*(2), 165–178. <https://doi.org/10.2478/v10053-008-0113-1>
- Spiegel, R., & McLaren, I. P. (2006). Associative sequence learning in humans. *Journal of Experimental Psychology: Animal Behavior Processes*, *32*(2), 150–163. <https://doi.org/10.1037/0097-7403.32.2.150>
- Stobbe, N., Westphal-Fitch, G., Aust, U., & Tecumseh Fitch, W. (2012). Visual artificial grammar learning: Comparative research on humans, kea (*Nestor notabilis*) and pigeons (*Columba livia*). *Philosophical Transactions of the Royal Society B: Biological Sciences*, *367*(1598), 1995–2006. <https://doi.org/10.1098/rstb.2012.0096>
- Straub, R. O., Seidenberg, M. S., Bever, T. G., & Terrace, H. S. (1979). Serial learning in the pigeon. *Journal of the Experimental Analysis of Behavior*, *32*(2), 137–148. <https://doi.org/10.1901/jeab.1979.32-137>
- Sun, R. (2001). Sequence Learning: From Recognition and Prediction to. *IEEE Intelligent Systems*, *August*, 67–70.
- Terrace, H. S. (1987). Chunking by a pigeon in a serial learning task. *Nature*, *325*(6100), 149–151. <https://doi.org/10.1038/325149a0>
- Terrace, H. S. (2005). The simultaneous chain: A new approach to serial learning. In *Trends in Cognitive Sciences* (Vol. 9, Issue 4, pp. 202–210). <https://doi.org/10.1016/j.tics.2005.02.003>
- Terrace, H. S. (2010). *The Comparative Psychology of Serially Organized Behavior*.

*Comparative Cognition & Behavior Reviews*, 5, 23–58.  
<https://doi.org/10.3819/ccbr.2010.50002>

Terrace, H. S., Son, L. K., & Brannon, E. M. (2003). Serial Expertise of Rhesus Macaques. *Psychological Science*, 14(1), 66–73. <https://doi.org/10.1111/1467-9280.01420>

Wallace, D. G., & Fountain, S. B. (2002). What is learned in sequential learning? An associative model of reward magnitude serial-pattern learning. *Journal of Experimental Psychology: Animal Behavior Processes*, 28(1), 43–63. <https://doi.org/10.1037/0097-7403.28.1.43>

Whiten, A. (1998). Imitation of the Sequential Structure of Actions by Chimpanzees (Pan troglodytes). *Journal of Comparative Psychology*, 112(3), 270–281. <https://doi.org/10.1037/0735-7036.112.3.270>

Whiten, A., Custance, D., Gomez, J.-C., Teixidor, P., & Bard, K. A. (1996). Imitative learning of artificial fruit processing in children (homo sapiens) and chimpanzees (pan troglodytes). *Journal of Comparative Psychology*, 110, 3–14.



## List of figures

**Figure 1.** Front part of the apparatus used in the test (Kea side).

**Figure 2.** Back part of the apparatus used in the test (Experimenter side).

**Figure 3.** The aviary's different area. The experiment was carried on in the *Porticula Res*, while the *Porticula Expectatio* had the function of waiting area for the birds.

**Figure 4.** The experiment setting: the apparatus seen from the experimenter's perspective inside the testing area, with the camera to record the results. The gate separates the waiting area from the testing compartment. The white panels visually isolate the whole area from the rest of the aviary.

**Figure 5.** The different arrangement of the sequences. Linear 1 and Random 1 start from the bottom, while Linear 2 and Random 2 start from the top. The number indicate the order in which the kea were trained to touch the lights. In the linear sequences the chunks are composed by the light 123-456-789.

**Figure 6.** On the x axis, the number of stages of the test; on the y, the number of total sessions needed by every bird.

**Figure 7.** The number of steps that compose the sequence is represented on x axis; the mean number of sessions needed to complete every stage is represented on the y axis.

**Figure 8.** The number of completed stages of both groups correlated with the birds 'age.

**Figure 9.** Cumulated number of successful trials for every bird for every stage before reaching the criteria.

**Figure 10.** Cumulated number of unsuccessful trials for every bird for every stage before reaching the criteria.

**Figure 11.** Number of successful and unsuccessful trials in every stage transformed in positive and negative number.

**List of tables**

**Table 1.** Individuals participating the experiment with their name, age at test time, sex, modality of rearing and correspondent sequence group of the test.

**Table 2.** Description and goal of every phase of the test.

**Table 3.** Completed stages and number of sessions for each bird.

**Table 4.** Number of sessions for each stage of the test in the linear and the random sequences and their mean values.

**Table 5.** Pearson's correlation between the depended and independent parameters.

**Table 6.** Mean number of trials for each stage separated for successful and unsuccessful