universität wien

MASTERARBEIT / MASTER'S THESIS

Titel der Masterarbeit / Title of the Master's Thesis

„Serial Reversal in ravens (*Corvus corax*)"

verfasst von / submitted by

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angestrebter akademischer Grad / in partial fulfilment of the requirements for the degree of

Master of Science (MSc)

Wien, 2022 / Vienna, 2022

Studienkennzahl lt. Studienblatt / degree programme code as it appears on the student record sheet:	UA 066 878
Studienrichtung lt. Studienblatt / degree programme as it appears on the student record sheet:	Masterstudium Verhaltens-, Neuro- und Kognitionsbiologie
Betreut von / Supervisor:	Univ.-Prof. Mag. Dr. Thomas Bugnyar

Acknowledgements

I would like to thank my supervisor Thomas Bugnyar first and foremost. He guided me from my initial interest of corvids to actual science and helped me from the first email onwards to find my footing. Without his encouragement and enthusiasm, I would likely not be writing about these experiments today.

Furthermore, I would like to thank Petra Pesak for her organisation as well as hard work to secure my place at the research station. Similarly, I would like to thank the team of the Haidlhof research station from all keepers (Flo, Gerald, Alpi, Julius, Claudia, Caro, Flo U.) for their constant presence, guidance, understanding, and just generally making me feel part of their team. Last but not least on the research team, I would like to express my gratitude towards András Péter who lived through all the iterations of my experimental setup and still had a smile on his face after installing them.

Next, I would like to thank Palmyre Boucherie for her guidance to becoming a researcher, both on a linguistic level as well as, most importantly, on a statistical one.

Also, I have to thank Lisa-Claire Van Hooland, Katharina Wenig, and Lisi Leitgeb, who were at the time of this theses like mentors and the loveliest company through my days of data collection.

Finally, I would like to thank my family. My mother, Doris Nagel, who read through all my works and always had an open ear to discuss the newest problems I was facing. My father, Martin Nagel, who believed in my choice of profession even if it is not the most stable one. My grandparents, Helga and Peter Nagel, who put up with exactly this change and still held their arms open when I started to get frustrated. Thank you for always being their for me.

Ultimately, I want to thank my partner, Thomas Filek. I think he got the brunt of the force of my struggles and was always by my side. Without him, I might not have been able to work through my insecurities and general confused organisation to finish this thesis.

Thank you all so very much.

Abstract

Learning flexibility has been previously linked with ontogenetical and social factors enabling animals to adapt and increase their chance of survival. Understanding the cognitive requirements and ensuing abilities is, however, often obscured by associative alternatives. This study aims to get a closer look at the factors playing a role in the abilities of learning and relearning patterns and the connected capabilities in the common raven (*Corvus corax*). Through a serial reversal task in which the subjects, upon learning a certain rewarded stimulus, needed to switch to the opposite of the two presented colours, forms of generalisation and learning abilities were measured according to the number of needed trials and errors until reaching the learning criterion. Confounding factors such as age, experience, sex, stress, and breeding status were subsequently excluded to be of a significant influence on the learning outcome. The mean improvement over the trials and the number of errors linearly decreased over the session of the experiment. This indicates that all ravens were able to successfully master the experiment and, hypothetically, were able to generalise a pattern over time. An overall tendency could be observed while individuals still presented a strong interspecific difference. Further research into the effect of personality, such as fast and slow learners or degrees of boldness, would be needed to gauge the exact factors for the found variance.

Lernflexibilität wurde früher mit ontogenetischen und sozialen Faktoren in Verbindung gebracht, welche es Tieren erlaubt sich zu adaptieren und ihre Überlebenschance zu steigern. Die kognitiven Voraussetzungen und die damit einhergehenden Fähigkeiten zu verstehen, sind jedoch oft schwer von assoziativen Alternativen zu unterscheiden. Diese Studie versucht sowohl einen vertieften Blick in die Faktoren der Fähigkeiten zu geben, welche eine Rolle beim Lernen und Wiederlernen von Mustern spielen, als auch die damit verbundenen Kompetenzen von Kolkraben (*Corvus corax*). Mittels einer serial reversal Aufgabe, bei der die Versuchstiere, sobald sie einen belohnten Stimulus erlernt haben, den jeweils anderen von zwei gezeigten Farben auswählen müssen, können Formen der Generalisierung und der Lernfähigkeiten gemessen werden, in dem die benötigten Versuche (trials) und Fehler (errors) bis zum Erreichen des Lernkriteriums ausgewertet werden. Möglicherweise signifikante Störfaktoren auf das Lernen wie Alter, Erfahrung, Geschlecht, Stress und Brutstatus konnten nachfolgend exkludiert werden. Die durchschnittliche Verbesserung über Versuche hinweg und in der Menge an Fehlern ist mit den Durchgängen linear weniger geworden. Dies zeigt, dass alle Raben fähig waren das Experiment zu meistern und hypothetisch Muster über die Zeit generalisieren konnten. Eine generelle Tendenz aller Individuen konnte aufgezeigt werden, während jedoch starke interspezifische Unterschiede auftraten. Weitere Forschung in Bezug auf diesen Effekt der Persönlichkeit, zum Beispiel bei schnellen und langsamen Lernenden, sollte eine bessere Einschätzung des Effekts auf die Varianz geben.

1. Introduction

1.1 Background

As humans we try to understand ourselves and our surroundings. We create meaning where often there is none, while bringing subjectively likely explanations together with irrelevant situations. Thriving to understand why and not only what (Hempel & Oppenheim, 1948). Memorising re-occuring situations and saving their outcome as connected has been of evolutionary importance (Riedl, 1979). Generally, research works towards this exact goal while trying to elicit a strong and abstracted and therefore objective link to action and cause. By using methods to exclude confounding factors and irrelevant assumptions, mostly one explanation should remain in the end through falsifying others (Popper, 1935). A mighty feat that often shatters at the very beginning: terminology. In this study, the idea and main argumentation is located in the field of cognition. This term alone has been under constant change in definition and appropriation to multiple aspects of research. It is widely used in science ranging from social capabilities of humans to the basic processing of surroundings in all animals. As a result, it encompasses not only the what but also the why. Some definitions include philosophical aspects such as intent and intelligence, others stem from empirical data resulting in properties such as memory and learning, and still more end in abstractions including problem solving flexibility and the processing of information (Theiner, Allen, & Goldstone, 2010). In all these cases, innate abilities such as reflexes and imprints are excluded from the term cognition to aid its distinction from the seemingly hard to distinguish word association (Buckner, 2015). Unsurprisingly, experiments in cognitive fields must usually be set up to negate pure associative processes as explanations (Buckner, 2015). Allen (2017) proposes that a single definition of cognition is wholly unnecessary as it is part of the research to find the limits of what can be categorised within this term. Humans have primarily been the keystone for defining cognitive abilities before a comparative approach was established (Zentall, Wasserman, Lazareva, Thompson, & Rattermann, 2008). The 19th century brought about a turning point by accepting other animals as at least equally crucial for our understanding (Staddon, 1983/2010).

In this study, the idea and main argumentation throughout is located in the field. As this thesis ' focus is not a philosophical one, a straightforward definition from Shettleworth (1998) will be used for further discussion stating that cognition includes “perception, learning, memory, and decision-making”.

Learning is inherently interwoven with cognition: a meaning is created simply from experiencing surrounding events and ultimately concludes in categorisation and a learned pattern (Hull, 1943; Zentall, Wasserman, Lazareva, Thompson, & Ratterman, 2008). This may be further analysed into subgroups ranging from learning purely from directly perceived action and result

combinations or go as far as eliciting meaning from relationships (Zentall, Wasserman, Lazareva, Thompson, & Ratterman, 2008). As a result, cognate animals are able to survive better by reacting faster to situations or become more flexible by being able to fall back to earlier experiences and solutions (Galef & Laland, 2005). This may be again achieved through direct experience or through observing others (Galef & Laland, 2005).

To understand the nature of these cognitive abilities, they are put into concepts to create a concrete idea of the observed disposition of the subjects (Honig, 1978). This enables researchers to find explanations for certain patterns of behaviours to specific stimuli (Hempel & Oppenheim, 1948). Often left to theory, a concept may only explain specific behaviours by observing many individuals in each setup (Honig, 1978). Nevertheless, finding patterns yields valuable insights into the various cognitive abilities of animals and through this furthers our understanding.

1.2 Test species - Common Raven (*Corvus corax*)

As early as the 18th century, avians have been acknowledged to be intelligent in the human eyes (Romanes, 1883/1977). Romanes (1883/1977) even described their brain as highly progressed in evolutionary terms. Specifically, ravens and crows have been researched extensively in the field of cognition. Myths and legends, such as the two ravens of Odin, had already conveyed this idea of corvids holding a wealth of wisdom and intelligence (Taylor, 2014). Looking at the physical properties, common ravens (*Corvus corax*) show a large brain comparable to the size ratio of chimpanzees (Jerison, 1973). Corvid cognitive abilities have been compared to be on a level of capuchin monkeys and chimpanzees including the rare ability of using and making tools implying causal reasoning and behavioural flexibility (Hunt & Gray, 2003; Emery & Clayton, 2004; Ottoni & Izar, 2008). They have been documented expressing the, caching with respect to a timeframe fitting the perishability as well as being aware of their social surroundings of conspecifics and their gaze (Clayton et al., 2001; Bugynar, Stöwe, & Heinrich, 2007). Unsurprisingly, the social behaviours of ravens have been of much interest. As a comparably long-lived species, multiple stages in life seem to contribute to the cognitive abilities as well as their survival when ultimately being pair bonded (Fraser, & Bugnyar, 2011; Roth, 2013; Hinde et al 2016; Boucherie, Poulin, & Dufour, 2018). However, especially early life experiences in their small families seem to have a strong initial effect on future cognitive and motor abilities (Fritz, & Kotrschal, 1999; Bugnyar, Stöwe, & Heinrich, 2007; Schwab et al., 2008). Furthermore, the highly complex fissure-fusion behaviour in non-breeding ravens has additionally yielded insights into social and cognitive capabilities of these animals (Braun & Bugnyar, 2012; Loretto et al., 2017). These competencies allow ravens to express a high flexibility both in context with conspecifics but also their environment (Sol, Timmermans, & Lefebvre, 2002; Miller et al., 2015; Miller, Schwab, & Bugynar, 2016). Learning from different sources can, therefore, be observed in ravens

and other corvids with the ensuing cognitive flexibility being an especially interesting field (Watanabe, 2012). One option to test this ability in a rather simple but effective setup will be discussed in this thesis.

1.3 Serial Reversal

In a serial reversal (discrimination) task, the individuals are usually presented with a choice of two differently coloured, positioned, or shaped targets in which one is set as the rewarded choice, while the other yields nothing (Terrace, 1963; Pubols & Benjamin, 1957; Shettleworth, 1998). After reaching a specific learning criterion of correct choices in a set number of repeats, the rewarded stimulus is reversed. For example, a choice of yellow and blue with the initially rewarded colour being blue, would then be switched to yellow being positively associated. This would then be repeated for a set number of sessions depending on the experimental species, setup, and timeframe. The reversal may happen during the same session while other setups end with hitting the learning criterion (e.g., Kirkish, Fobes, & Richardson, 1979). The working memory of the subjects is activated to remember a certain previously encountered pattern to succeed in subsequent ones (Honig, 1978).

The results of this experimental outcome were discussed to have different meanings depending on the initial hypotheses. At first, they were thought to enable a better understanding of cognitive evolution from more basal groups leading to derived ones (Kendler, 1959). Subsequently, a multitude of different species ranging from invertebrates, such as cockroaches (Longo, 1964) or octopi (Boycott & Young, 1958), to all vertebrates, such as fish (e.g. Bitterman, Wodinsky, & Candland, 1958), amphibians (e.g. Seidman, 1949), reptiles (e.g. Holmes et al., 1966), birds (e.g. Bullock & Bitterman, 1962), and mammals (e.g. Warren, 1966) were tested. However, a simple evolutionary and phylogenetic answer could not be proven across all tested species and led to the further assumption that favourable outcomes of quicker learning times and less mistakes are rather linked to learning flexibility (Watanabe, 2006). Here, the initial acquisition of learning a certain rewarded stimulus would be compared to all further reversal results to gauge this ability (Rayburn-Reeves, Stagner, Kirk, & Zentall, 2013). A certain win-stay lose-shift strategy, employed by many flexible species, was assumed as a basis for this quick adaptation to the experiment (Shettleworth, 1998). Expanding on this capability and depending on the learning curve, the subjects would show, with a strong decrease of needed trials for each reversal over time, a form of generalisation (Barrows, 2011).

Corvids are known to be able to remember certain caches and whether or not they have retrieved the items enabling them to use an episodic-like memory knowing what, where, and when something was hidden at a certain location (Clayton et al., 2001; Bugnyar & Kotrschal, 2000; Bugnyar, Stöwe, & Heinrich, 2007; Raby & Clayton, 2010). The basic tendency to look for food

that had been hidden by another would retrieve knowledge from the long-term memory would use habits, while learning the correct stimulus, the working memory (Anderson, 1983/2013). Additionally, past research has shown that many corvid species, such as jays, are able use generalised learning strategies to succeed in serial reversal tasks indicating a likely connection between flexibility of behaviour and social context (Bond, Kamil, & Balda, 2007). While ravens show a much larger brain to body size ratio to these species, the learning outcome may not be inferred simply from this parameter (Boussard, Buechel, Amcoff, Kotrschal, & Kolm, 2020). Ultimately, looking at a further corvid species, ravens present an enticing addition to test the limits of this experimental setup to get a closer look at the cognitive processes of learning flexibility of a highly social animal.

1.4. Hypothesis

The aim of the thesis is to yield information on problem solving strategies, the influence of past experiences, social influence, and learning flexibility and their connection to personal preference, age, and experience across the tested individuals. This leads to the following predictions: Subjects employing a win-stay lose-shift strategy would quickly change from an unrewarded choice showing impulse restraint and activating the working memory rather than choosing according to habit (Hassett & Hampton, 2017). Those with previous experience and, in this context, older would show no difference in the learning curve when compared to inexperienced individuals if learning flexibility is dependent on working rather than long-term memory. Generally, a quick decrease in needed trials and errors across all ravens should be observable due to their cognitive abilities. However, an individual variance should be encountered on a subject level due to personality and learning style.

2. Methods

2.1. Subjects

All 11 study individuals were common ravens (*Corvus corax*), with six female and five male subjects (Tab. 1). Six of them were considered active breeding pairs and housed in separate aviaries (10x7m) with the rest being categorised as non-breeders, all kept in one large aviary with a total of 12 ravens (18x15m) (Fig. 1). Individuals were differentiated by differently coloured rings on the legs. Two individuals were without rings as their legs were treated at the time of the experiments. As they were housed in different aviaries, no distinction problems would occur. Non-breeder subjects 'age ranged from one year to 3, while breeders were 9 to 11 years.

All aviaries are located outdoors at the Haidlhof Research Station of the Department of cognitive biology of the University of Vienna. The ground was covered with a mixture of sand, gravel, and grass and included a variety of trees, tree trunks, wooden perches, swinging branches, and objects for enrichment such as shoes, toys, and clothing. Furthermore, parts of the enclosure had roofing and walls for protection against rain and the cold. Breeding aviaries included a nesting box. The home aviaries included an experimental chamber and could fully be closed off by two swinging doors to be out-of-sight for other subjects (Fig.1, grey areas). This part of the aviary was always fully roofed. As a result, all ravens were familiar with the location of the study. All subjects were fed twice a day with a mixture of different meats, other sources of protein, grain, oats, vegetables, and fruits. Water was provided ad libitum and cat treats given for

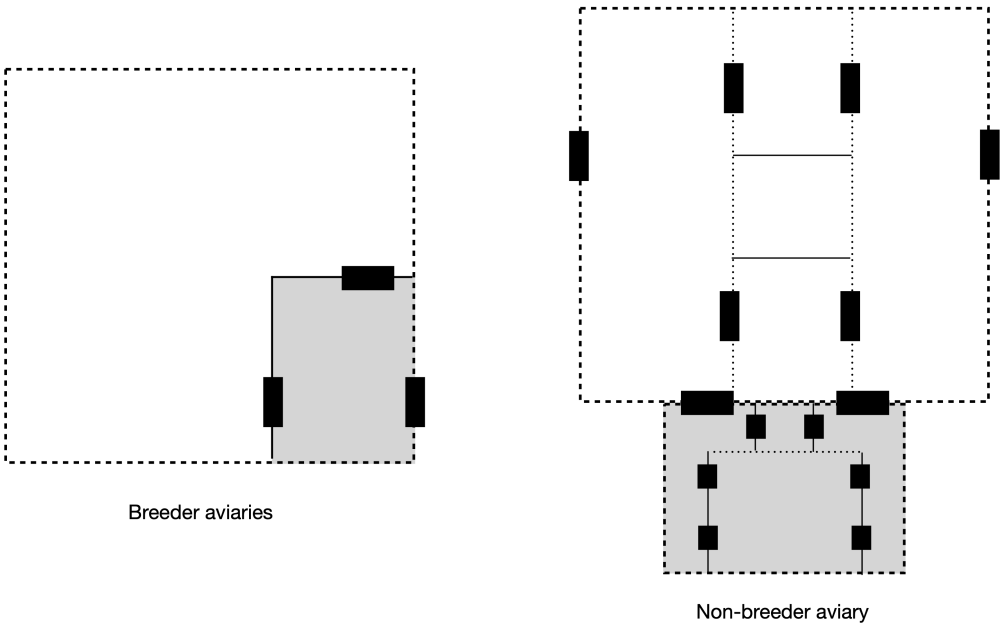

Figure 1: Aviaries and adjoining experimental compartments (grey) of the breeding and non-breeding ravens. Breeder aviaries (left) house a breeding pair of two ravens, while the non-breeding aviary houses 12 not pair bonded sub-adult ravens. Experimental compartments are always open outside of experiments and available to the individuals. Dotted lines indicate a wire mesh fence, while full lines obstruct the sight.

encouragement in training for commands on a regular basis. As an experimental reward, all animals were provided with soft dog treat rings (Frolic) cut up into eights. All subjects were not food-deprived with the offered treats being an additional food source.

All individuals were unfamiliar with the serial reversal apparatus, however, already encountered a single reversal task in previous experimental setups as well as being used to participating in other studies with humans. Subjects were free to choose whether to participate on any given day and entered the experimental compartment willingly or not. If a raven decided to ignore the experimenters coaxing, the study day would be shifted to another.

Table 1. List of tested individual characteristics such as name, sex, birth year, breeding status, breeding partner if applicable, and ring colour to identify the subjects.

INDIVIDUAL	SEX	BIRTH YEAR	BREEDER	BREEDING PARTNER	RING COLOUR
Joey	f	2010	yes	Rocky	none
Rocky	m	2012	yes	Joey	thin silver
Nobel	f	2012	yes	George	orange
George	m	2012	yes	Nobel	white
Astrid	f	2010	yes	Horst	red
Horst	m	2012	yes	Astrid	silver
Quito	m	2020	no	none	yellow
Kofi	m	2018	no	none	large green
Kai	f	2018	no	none	red-white spiral
Zazou	f	2020	no	none	none
Murphy	f	2018	no	none	blue

2.2. Experimental apparatus

For the setup a hole was cut into one wireframe of the experimental compartment. A wooden board was mounted on a fixed piece of wood with half inside and half outside the aviary in the mentioned cavity (Fig. 2). In between the experiments this gap was covered with a small piece of

Figure 2: Wooden boards fixed half inside and half outside of the experimental compartment. Left: Fixed board inside of the breeding aviaries with the box for obstructing sight as well as the experimenter behind seated on a styrofoam block. The small wire mesh door and hole can be seen above the board to insert the experimental board. Right: Fixed wooden board on ledge inside the non-breeder experimental compartment with box for obstructing sight on the right and the experimenter standing behind. The small hole above the board to insert the experimental board can be seen.

mesh fixed with zip ties and spring hooks. The board was either approximately 1.40cm high fixed onto a ledge for the non-breeders or about 20 cm above ground level fixed to a wooden block for the breeders with the experimenter standing or sitting on a small block of hard Styrofoam respectively (Fig. 2). Non-breeders were able to either fly up to the ledge or jump onto branches first, while breeders were directly able to interact with both targets from one spot on the ground. The height difference was chosen purely due to the ravens 'preference encountered during the habituation phase and had no other influence on the subjects 'likelihood to interact with the apparatus.

On top of the wooden board, a second panel made from chipboard could be slid inside to the aviary half. This part included two small cut-outs (diameter ca. 3.8 cm) with inserted opaque cups where rewards could be placed and covered without being visible from outside (Fig. 3). These openings would be closed with the targets which were made up of one wooden disk (diameter 6 cm) fixed onto a wooden stick (length 40 cm) each. The disks were painted a standardised yellow (R=255, G=192, B=0) or blue (R=79, G=129, B=189), determined by their red (R), green (G), and

blue (B) values. To hide the panel when the target sides were swapped or the rewards inserted, a cardboard box was either put below the main board or next to it.

Figure 3: Experimental boards with coloured (yellow/blue) targets on sticks with cups and rewards. Left: Breeding aviary with individual Horst standing in front of the apparatus during habituation with both cups rewarded. Right: Non-breeding aviary experimental compartment with individual Quito during reversal session, choosing one target on top of the ledge.

2.3. Habituation

All ravens were already familiar with the experimental chamber and the opening and closing of the necessary doors requiring no additional habituation for separation.

The individuals were introduced to the movable parts of the apparatus approximately a month before the actual start of the study. At the same time, the fixed board was installed, the opening cut out, and the closing mechanism fitted. About a week after, the first individuals were exposed to inserting and removing the chipboard panel with the targets. Another seven days later, all subjects were shown a treat inside both cups with the targets covering them. At this point some ravens were already flipping the wooden disks and interacting naturally with the board even when being removed. As soon as no immediate retreat from the apparatus was perceived, the subjects would start with the first phase of testing. Depending on the individual, this would take up to another week.

2.4. Time frame

The data collection spanned from November 2020 until October 2021. The long-time frame stems from some individuals being unavailable during the breeding season. Testing was usually

done from Monday to Friday between 9am and 3.30pm with a few taking place over the weekend due to unforeseen circumstances making it not viable to hold experiments during the week. All individuals were tested once per day and ran through no more than one reversal. Sessions lasted from 5 to 60 minutes depending on the subjects 'motivation, external influences, such as noise and weather, and success. If a raven would not participate for more than 15 minutes or showed signs of stress, the session would be stopped for the day. All individuals were tested this way at least three times a week and needed approximately one session to complete a reversal. This would amount to a mean duration of five weeks per individual for the whole serial reversal experiment.

2.5. Recording

All recordings were done through a dome camera which would be activated that would film the experiment from above, focused on the apparatus. These cameras had already been installed inside of the experimental compartments before this project. The focus can be moved from a computer outside of the aviaries. Movement and capture of the filming material yields no reaction from the ravens and was therefore deemed as no distraction. After the experiment session, the recording could then be directly cut down to the session length and uploaded to the server and the coding software. This was done immediately after the experiment day.

2.5. Procedure

For each individual a randomised starting colour would be chosen so that an equal number of ravens would start with either blue or yellow as the rewarded target. The serial reversal would then be categorised into 16 reversals in total with the first one being the initial acquisition (IA) and all subsequent ones simply named reversals including their number (e.g., R1 for the first reversal after the IA). After each correct colour choice (S+), the raven would pick out the treat and the panel with the two targets (from now on only called apparatus) would be retrieved and hidden inside of the cardboard box. According to a pseudo-randomised list that indicated which colour would be put on either side, the cup underneath the S+ coloured target would be baited and both cups covered. The choice would also be noted down with X marking an S+ and O marking a wrong choice (S-). Upon an S-, the side configuration would not be changed. Afterwards, the apparatus would be reinserted for the raven to choose again. After 17 out of 20 S+ choices, the session would stop and the colour reversal (blue to yellow S+ or yellow to blue S+) would follow for the next one.

The general procedure of one session would therefore work according to the following steps. First, the dome cameras would be focused to the correct spot and the recording started. Second, the apparatus, the rewards, the hard Styrofoam sitting block, the randomised list, a notebook for

the results, a pen, and a pair of sunglasses were all transported inside the cardboard box to the aviaries at the start of the session. Before separation, all material was set up and prepared in front of the fixed board with the reward being inserted into the appropriate cups outside of view and inside of the front-opening cardboard box. Third, the individual was separated inside of the designated compartment by the experimenter. Afterwards, the wireframe door would be opened, and the starting time indicated on the notebook. The experimenter would then wear a pair of sunglasses to exclude any eye movement interfering with the ravens 'choice. The session would start immediately on inserting the panel with the coloured targets. After a maximum of 60 minutes or when successfully hitting the learning criteria, the apparatus would be retrieved one last time, the wireframe would be closed and finally the doors of the experimental compartment opened, so that the raven would be free to leave. This would then be repeated for all individuals tested on that day. At the end, the testing equipment would be stored in a dry cupboard and the cameras stopped. The videos were then cut down to the appropriate length and uploaded to the server.

All tests were done by the same experimenter and the order the individuals were tested in was pseudo-randomised by using the randomise function of R.

2.6. Data management

The written data from the notebook was transferred to a spreadsheet which was double checked through the recordings. All subsequent statistical tests were done using RStudio 1.3.1093 (R_Studio_Team, 2019) with R 3.6.2 (R_Core_Team, 2021) as a base. The data was categorised into four phases: P0 included only the IA, P1 reversals 1 to 5, P2 reversals 6-10 and P3 reversals 11-15. This would allow a clearer analysis of the learning effect over time. To calculate the reversal index (RI) the following equation was used:

$$1 + meanTTCphaseX/1 + TTCphase0$$

TTC is defined as the trials to criterion of the reversal for each phase (X = placeholder for phase 1-3, 0 = initial acquisition phase). This measurement is deemed to represent reversal learning severity (Rajalakshmi & Jeeves, 1965). All trials were visually represented using the R package ggplot and analysed through a one-sample Wilcoxon signed-rank test. This statistical method was also used as a post-hoc test to ascertain differences between the different phases. Performance differences across the phases of all individuals were calculated using the Friedman test and visually represented as violin graphs with boxplots using the R packages ggplot and Hmisc. To gauge the correlation of errors and trials, the Spearman rank test was conducted and plotted as a scatter diagram using the R package ggscatter.

3. Results

3.1. Total trials

Looking at the overall trials and the calculated mean, a trend can be seen in which the IA yielded a comparably low number in respect to R1 (Fig. 4). Over the course of the 15 trials, the amount of trials needed decreased across all ravens. The lowest number of trials was recorded

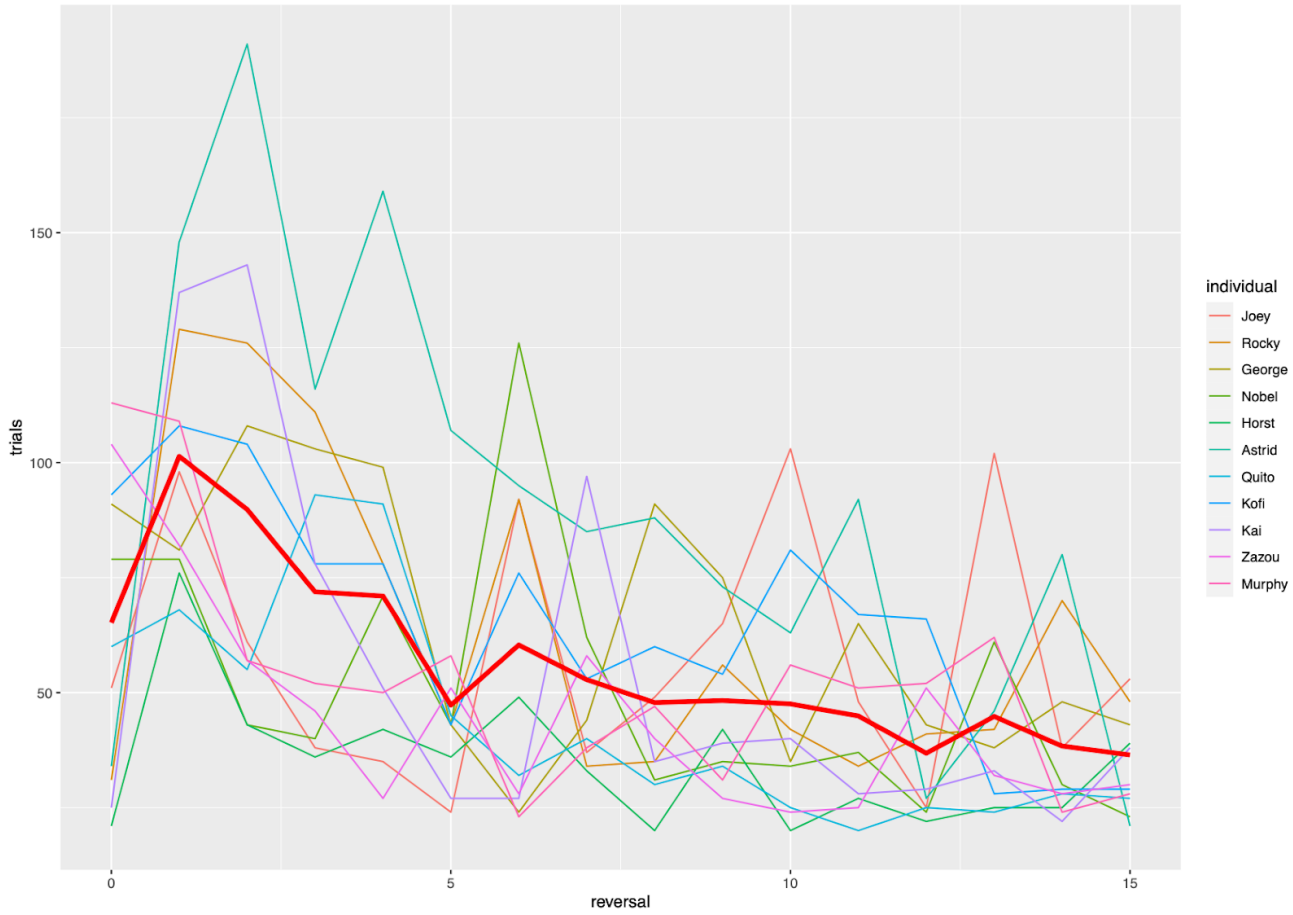

Figure 4: Learning curve expressed as trials across sessions (reversals) from initial acquisition (0) to 15th reversal (15). Colours represent the 11 tested individuals (light red = Joey, orange = Rocky, olive = George, green = Nobel, blue-green = Horst, turquoise = Astrid, light blue = Quito, blue = Kofi, violet = Kai, magenta = Zazou, pink = Murphy). The thick red line indicated the mean of all individuals.

for Horst with needing exactly 20 trials to reach criterion directly followed by Nobel with only 23. Some individuals such as Kofi and Joey display a high variance in their trials across sessions, but most others showed the expected learning curve with a stark decrease of needed trials until the last reversal. A clearer but similar picture can be observed when looking at the errors across the sessions. Here almost all individuals showed less errors across the reversals while having an initials spike in the earlier reversals (Fig. 5). No subject seemed to be unable to learn the serial reversal task, while the data signifies a strong individual difference in the success of the task. With the exception of Joey, who as previously mentioned also showed a high variability across the sessions, the calculated RI show that all other individuals presented lower scores for the last

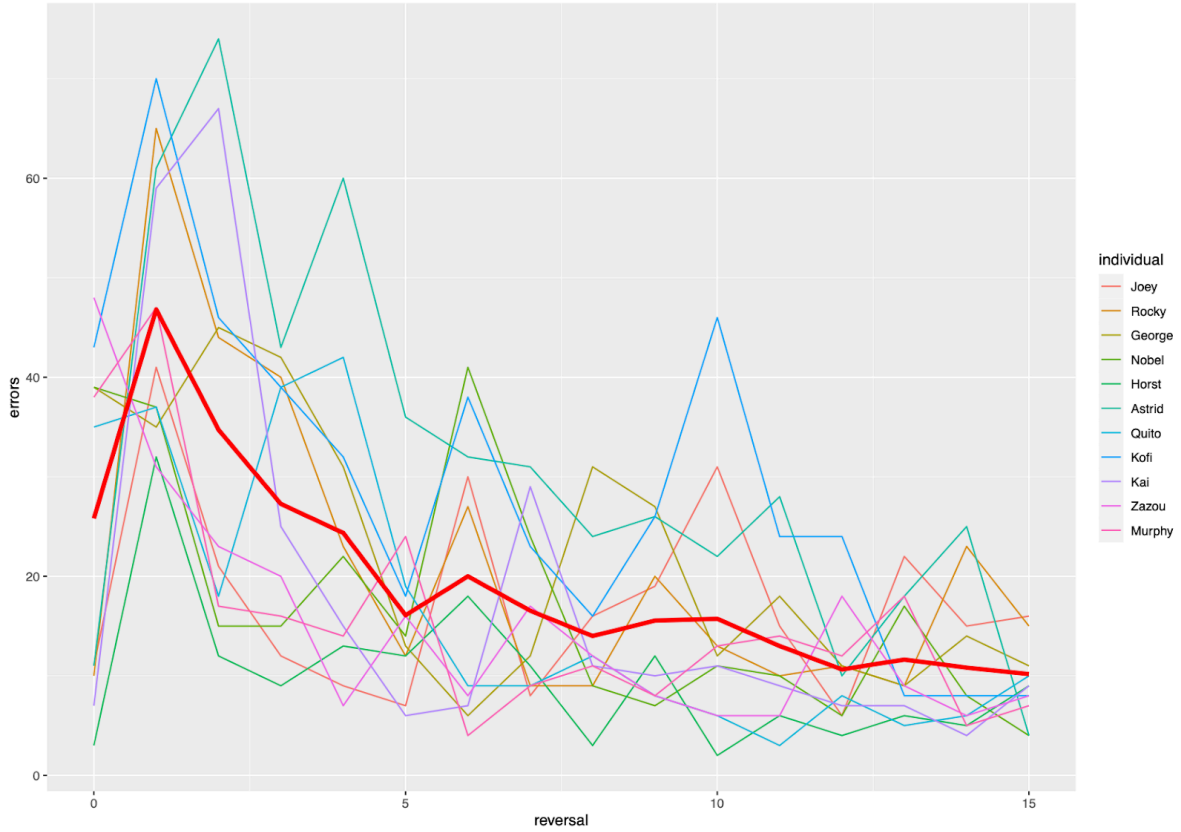

Figure 5: Learning curve expressed as errors across sessions (reversals) from initial acquisition (0) to 15th reversal (15). Colours represent the 11 tested individuals (light red = Joey, orange = Rocky, olive = George, green = Nobel, blue-green = Horst, turquoise = Astrid, light blue = Quito, blue = Kofi, violet = Kai, magenta = Zazou, pink = Murphy). The thick red line indicated the mean of all individuals.

phase compared to the first (Tab. 2). Murphy was the only individual showcasing the lowest score during phase 2. The biggest improvement could be found in Astrid with a difference of 2.6 from first to last phase, while Zazou only improved with a difference of 0.18. Notable is that this individual had the overall lowest initial and end score of the RI.

Table 2: List of reversal indices (RI) of each phase (RI Phase 1 = reversal 1-5, RI Phase 2 = reversal 6-10, RI Phase 3 = reversal 11-15) according to individual and their sex. Asterisk (*) indicates breeding pair status.

INDIVIDUAL	SEX	RI PHASE 1	RI PHASE 2	RI PHASE 3
JOEY*	f	1.00	1.35	1.04
ROCKY*	m	3.08	1.65	1.5
ASTRID*	f	4.15	2.34	1.55
HORST*	m	2.1	1.5	1.3
NOBEL*	f	0.70	0.73	0.45
GEORGE*	m	0.95	0.60	0.53
QUITO	m	1.17	0.54	0.42
KOFI	m	0.89	0.70	0.52
KAI	f	3.39	1.87	1.19
ZAZOU	f	0.51	0.35	0.33
MURPHY	f	0.58	0.35	0.39

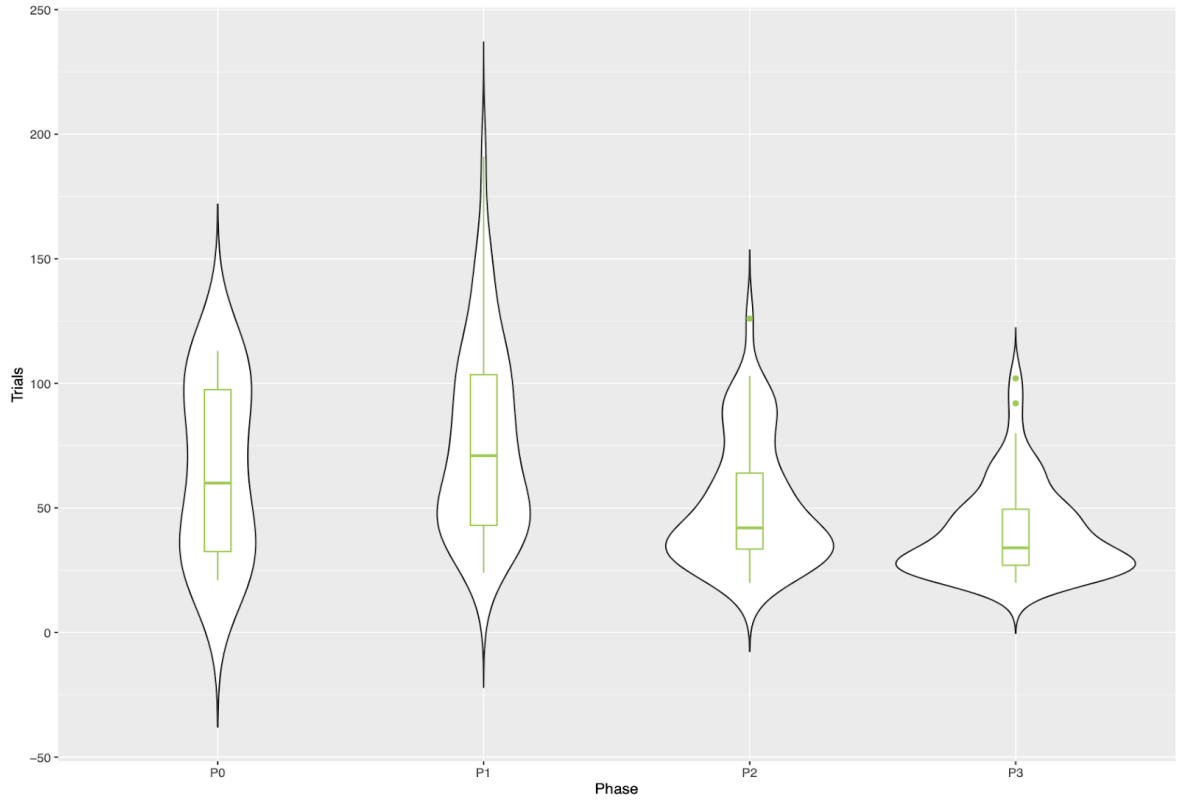

Figure 6: Violin plots with integrated box plots for the total number of trials needed across the four different phases (P0 = IA, P1 = reversal 1-5, P2 = reversal 6-10, P3 = reversal 11-15). The width of the plots indicates the distribution of occurrences of a certain number of trials needed, while the box plots showcase the distribution in quartiles as well as the median as the thick line.

The one-sample Wilcoxon signed-rank test showed no difference between P0 and P1 ($p=0.404$), while there were significant changes from P1 and P2 to latter phases ($n=11$; P1-P2: $p<0.001$, P1-P3: $p<0.001$, P2-P3; 0.030). The Friedman test furthermore showed significant performance differences of both errors ($n= 11$, $\chi^2 = 48.578$, $df= 3$, $p>0.001$) and trials ($n= 11$, $\chi^2 = 40.359$, $df= 3$, $p<0.001$).

The violin plots visualise these results as the distribution distance and size of quartiles are the largest in P0 for both analysed categories (Fig. 6, Fig. 7). Especially the median of the errors in this phase shows a great shift towards a higher number. In comparison, in both cases we can see a continuous decrease in distribution and variance towards P3. Additionally, this linear decrease across sessions was also found between trials and errors (Fig. 8). The Spearman rank correlation ($rho= 0.965$, $n= 11$, $p<0.001$) resulted in a significant correlation meaning that less trials meant less errors across all individuals

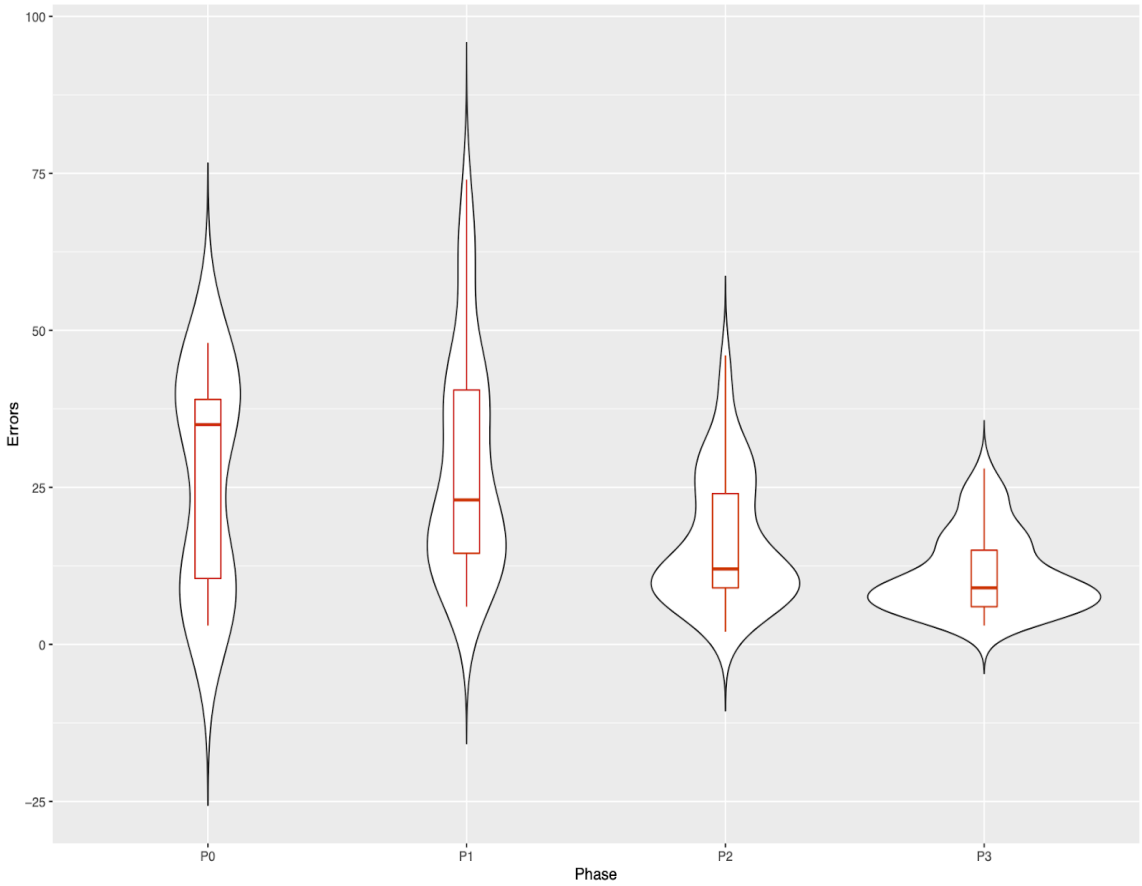

Figure 7: Violin plots with integrated box plots for the total number of errors needed across the four different phases (P0 = IA, P1 = reversal 1-5, P2 = reversal 6-10, P3 = reversal 11-15). The width of the plots indicates the distribution of occurrences of a certain number of trials needed, while the box plots showcase the distribution in quartiles as well as the median as the thick line.

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Looking at the possible confounding factors, the one-sample Wilcoxon signed rank test did not yield any significant results for an influence of sex (p= 0.824). In comparison, the influence of experience in the form of performance differences between non-breeders and breeding pairs with a mean age difference of 9 years did show a tendency towards quicker and more accurate trials by older individuals (p=0.0670).

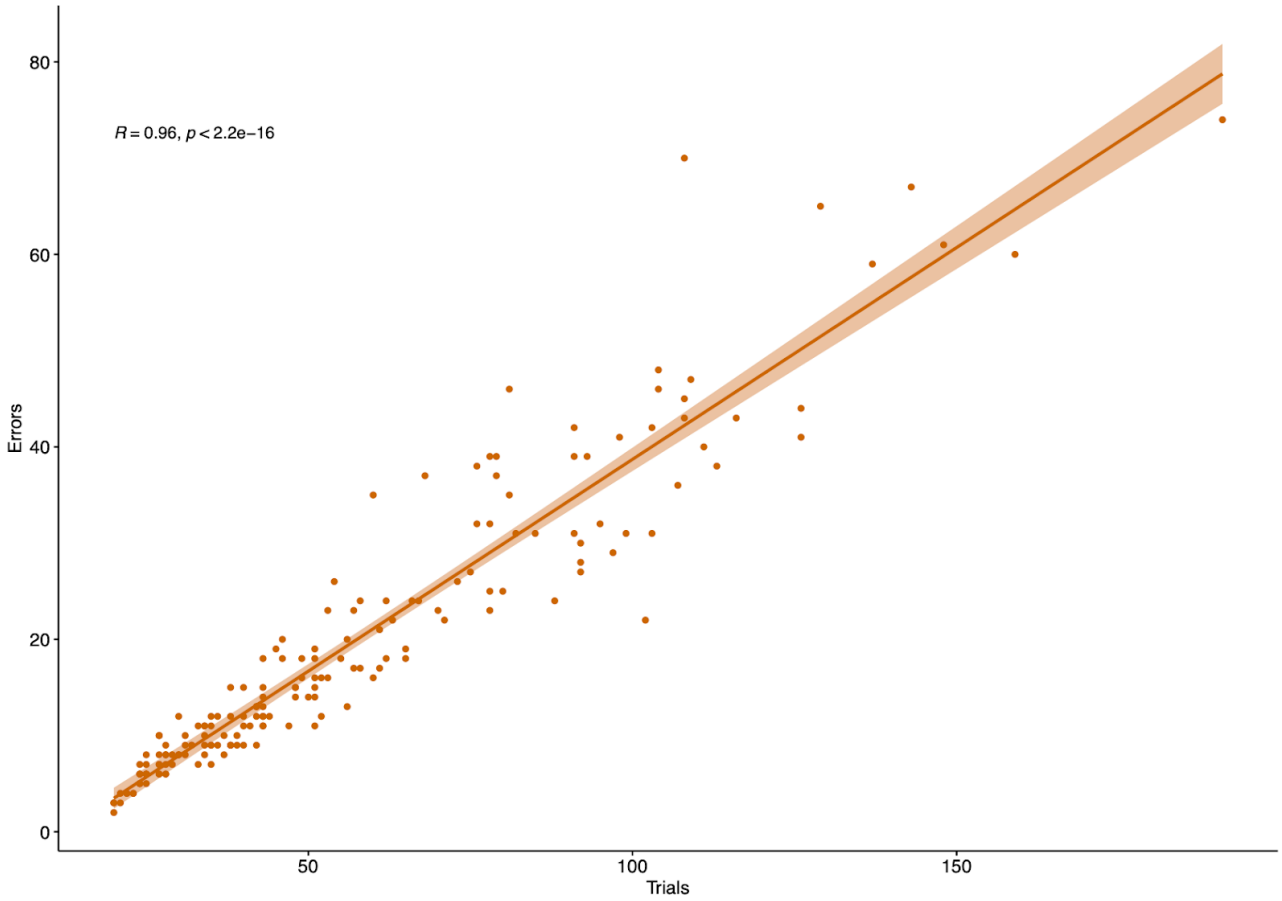

Figure 8: Correlation between all needed errors and trials to reach the learning criterion (17/20) of the last reversal using the Friedman test. The positive linear relationship of the two categories is shown through the red regression line. The orange area visualises the strength of the correlation. Each data point is expressed as a small orange dot. The Friedman test rho (rho= 0.96) and the p-value (<0.001) are noted in the top left corner.

4. Discussion

4.1. Main discussion

The results show that overall, all ravens were able to succeed in and learn the serial reversal task. The number of trials and errors decreased after an initial increase linearly (Fig. 1 and 2). The reversal learning indices support this across all three phases with the last one presenting the lowest score for all subjects (Tab. 2). Through impulse control, the ravens were therefore able to stop and choose carefully which target was the rewarded one, rather than picking the first one close to them (Dufour et al., 2012; Hillemann et al., 2014). Over the course of the sessions, the initial acquisition phase showed a wide spread of needed trials and presented errors until the learning criterion was reached (Fig. 3 and 4). Comparing this to the last phase, the distribution is much tighter and less outliers among the individuals 'success has been recorded. Consequently, they were capable of breaking a learned pattern, like a habit, to relearn the new rewarded stimulus with high accuracy (Harlow, 1949; Buytendijk, 1930). The decrease in the learning curve shows the learning pattern of the individuals in which the amount of trials is positively correlated with the amount of errors (Fig. 5). Over the course of the experiment, all subjects made less errors and needed subsequently less recasts of the same configuration. At the end, most completed one reversal per session needing less than 30 trials in comparison to the maximum of 191 in phase 1 (Fig. 4). The social and environmental flexibility of the highly cognitive raven seems to be reflected in the observed learning flexibility (Sol, Timmermans, & Lefebvre, 2002; Miller, Schwab, & Bugnyar, 2016). The closely related azure-winged magpies (*Cyanopica cyana*) showed a similar learning pattern in a serial reversal task, both in trial numbers, error count, and correlation of the two (Leitgeb, 2019). Three North American Corvid species (pinyon jays, *Gymnorhinus cyanocephalus*, Clark's nutcracker, *Nucifraga columbiana*, and western scrub jays, *Aphelocoma californica*) equally fit the results of this task while furthermore improving more quickly with increasing anticipated behavioural and social flexibility of each species (Bond, Kamil & Balda, 2007). In primate research, the serial reversal task was used as a basis to understand which area of the brain was important to form and use prior beliefs to complete the experiment (Jang et al, 2015). Macaque monkeys and common marmosets were shown to express most activity in the prefrontal and orbitofrontal cortex, the latter being of great importance for social learning (Ridley et al., 1985; Rygula et al., 2010; Gariépy et al., 2014). This ability is strongly evident in ravens, especially in non-breeders leading to long-term memorisation (Bugnyar, Stöwe, & Heinrich, 2007; Schwab et al., 2008). As a result, the assumption that this characteristic may be an indication for their success in a serial reversal task is likely.

While the difference in age has not yielded a direct result, it highlights a tendency of middle-aged ravens learning a miniscule amount faster than those younger. These would have been part

of other experiments including short serial reversals in other contexts but not as elaborate as this study. This may have resulted in slightly better selection as they were more familiar with the setup. However, no ravens were naive to serial reversals altogether. While some animals, such as dogs, decrease in their cognitive abilities comparable to humans and primates, this effect would not be present in the subjects of the experiment (Van Bourg & Wynne, 2021). Even the oldest raven with 12 years during the sessions would be categorised as middle-aged. This adult stage is especially linked to a peak in cognitive abilities and would be another explanation of the slight increase in performance (Van Bourg & Wynne, 2021).

Hormones have been shown to be a strong influence on performance but are unlikely to have had an effect during the experiment as all breeding pairs were tested outside of breeding season and all non-breeders expressed no behaviours that would fall under this category, such as nest building or territoriality (Stöwe et al., 2008; Bebus, Small, Jones, Elderbrock, & Schoech, 2016). For one breeding pair, George and Nobel, a pause in the middle of the reversal had to be allowed as the experiment could not be completed before this time but took up the remaining sessions quickly after the four-month break with only a slight initial increase seen around reversal 7 (Fig. 1 and 2). The birds seemed to have retained much of their knowledge of previous reversals in their long-term memory, similar to other research done on rats and bumblebees (Calhoun & Handley, 1973; Chittka, 1998). This points again to the likelihood of older ravens showcasing a slight improvement over younger more inexperienced ones through previous encounters with similar setups. Stress related patterns may be excluded as detrimental factors for variation in the results as all sessions were cut short if signs of tension were observed (Munteanu, Stocker, Stöwe, Massen, & Bugnyar, 2017). Individuals with a higher variation in success, such as Joey and Kofi, also outperformed others in certain reversals further strengthening this assumption (Fig. 1 and 2).

There was no documented difference between the sexes contrasting other experiments in which especially females presented a higher flexibility, while males proved to be faster learners (Range et al., 2006; Lucon-Xiccato & Bisazza, 2017). Rather, the differences in roles among the pairs would explain varying cognitive capabilities (Fuss & Witte, 2019). However, as ravens form long-term monogamous pair bonds supporting each other, it would be detrimental for survival if one sex would be inferior in abilities making it unlikely that a universal difference among males and females is probable in this species (Clayton & Emery, 2007).

This leaves a personality difference as the most likely deciding factor for the variance in individual success. The strong individual difference seen both in the distribution of the trial-and-error amounts in the phases and the irregular peaks of subjects like Joey could be an indicator for this. The mean does express the general tendency across all tested subjects but is not representative of results for specific reversals. Research in great tits (*Parus major*) has shown that individual differences in learner types significantly influences the approach to new tasks independent of age and sex (Dingemanse et al., 2003; Groothuis & Carere, 2005). Ravens were

observed to have similar personality traits in a context of novel objects in which their approach was stable across time on a gradient of bold to timid (Stöwe et al., 2006). This follows that the information received and then used may heavily depend on personal characteristics and not only on learning capabilities. The differences in the number of trials and errors are therefore likely to vary on an individual level while overall representing the general leaning flexibility of the group (Miller, Schwab, & Bugnyar, 2016; Smit & van Oers, 2019). For a closer look at the specific influence of personality and the personal approach towards problem-solving, individuals would need to be tested in setups that may gauge the learner type before further testing of specific abilities. Especially regarding the individuals' ontogeny, the impact of the sibling and parental upbringing and the resulting social competencies may yield further insights into the cognitive abilities that ravens present during experiments.

4.2. Conclusion

To conclude, all ravens showed to be able to learn the serial reversal task. They expressed a degree of learning flexibility by switching from one target to the other as well as generalising a pattern across the experiment. The trials and errors were significantly similar across the whole group of subjects with errors and trials decreasing at a constant rate over the full 15 sessions. Nevertheless, some individuals showed a strong individual variance in their results. Among them, factors such as age, experience, stress, or breeding status had no significant effect on the results. Therefore, the most likely explanation is an individual difference among the subjects that shaped their learning curve, which has yet to be explored in more depth.

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