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„Serial reversal learning in the azure-winged magpie (*Cyanopica cyana*)“

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Elisabeth Barbara Leitgeb BSc

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1 INTRODUCTION

1.1 Cognition & Flexible Behaviour

In the recent years there is a growing interest in the topic of cognitive abilities in birds. Within literature, a diversity of definitions regarding cognition can be found (for an overview see e.g. Barrows, 2011). That is because historically, mental capacities and thereby cognition were surveyed separately, and with various approaches by two different disciplines (Mills, 2010; Shettleworth, 1998, 2010). Only since the 21th century the two branches, consisting of psychologists, who studied the underlying neural mechanisms (i.e. Tinbergen's proximate level), and ethologists, which were interested in the animal´s behaviour in its natural environment (i.e. the ultimate level), integrate each other (Mills, 2010). According to Shettleworth (1998, 2010), the term cognition can be defined broadly as the underlying processes of an animal's gathering and using of local environmental information. Moreover, it includes the handling and recalling of this collected information (Shettleworth, 1998, 2010). In a less broad sense, cognition refers to the usage of declarative knowledge (i.e. explicit 'knowing that'; McFarland, 2014; Shettleworth, 1998, 2010). Furthermore, it comprises issues concerning the sensory systems, perception, learning, as well as communication – all leading to decision making (Mills, 2010; Shettleworth, 1998, 2010). Consequently, these cognitive mechanisms help remembering past incidents, plus choosing present and subsequent actions and reactions (Wasserman & Zentall, 2006). Intelligence is the capability of flexibly conveying and using such cognitive skills, in order to solve other problems than these skills evolved for (Emery, 2016).

The ability of reacting flexibly to both, environmental as well as social challenges, is considered as adaptive (Delius, Siemann, Emmerton, & Xia, 2001), as it can positively affect a creatures survival (Roth, 2013). Flexible behaviour reflects an important type of cognition, and is also part of the executive functions (Güntürkün, 2005). This term refers to an individual's capability of adjusting its behaviour towards environmental conditions, and it employs shifting established responses to known stimuli, as well as the creation of novel responses to new types of stimuli (Leal & Powell, 2012). Furthermore, flexible behaviour requires the skill to reverse options while a new information is learned (Badre & Wagner, 2006). For example, seasonally caused environmental changes can alter food availability, and

thereby demand flexible adjustment of the behaviour (Komischke, Giurfa, Lachnit, & Malun, 2002). Besides this, living in complex social groups requires individuals to flexibly adjust to the behaviour and intentions of others (Reader, 2003). Also the successful dispersal in new environments (Sol, Timmermans, & Lefebvre, 2002) as well as innovations and learning are supported by the species' mental flexibility (Watanabe, 2012). Though, being flexible is more costly than being immutable (Watanabe, 2012). From the evolutionary perspective, cognitive abilities are traits where natural selection works upon, and consequently specialisation happens: a more and faster changing environment would favour species that exhibit more flexible behaviour (Bond, Kamil, & Balda, 2007; Mills, 2010).

1.2 Serial Reversal Learning

There are several methods how to test behavioural and thereby mental flexibility in humans and other animals (Audet & Lefebvre, 2017; Watanabe, 2006). Reversal Learning (RL) is one such paradigm (Day, Crews, & Wiczynski, 1999; Rayburn-Reeves, Stagner, Kirk, & Zentall, 2013). In this task, initially, a discrimination between two differentially rewarded stimuli has to be learned, followed by a reversal of the former reward contingencies (Audet & Lefebvre, 2017; Davey, 1989; Shettleworth, 1998, 2010). In other words, during the acquisition of a RL, task a subject learns the associative discrimination between two defined stimuli A and B: one stimulus is rewarded (positive stimulus, "S+"), the other one is not (negative stimulus, "S-") (Audet & Lefebvre, 2017; van Horik & Emery, 2018). These stimuli can either be presented separately in two sequential trials (=successively), or both together in one trial (=simultaneously) (French, 1965; Mackintosh, 1974). After a certain number of trials or when the subject reaches a criterion, the reward contingencies (=reinforcement allocation) are reversed to the opposite (i.e. Reversal) (Bitterman, 1965; Shettleworth, 1998, 2010). This implies the subject to be exposed to the same stimuli again in the reversal, but when for example A was initially S+, it becomes S- and B gets rewarded instead (Davey, 1989; Delius & Delius, 2012; French, 1965). Consequently, it has to inhibit the original rewarded response and form a new association (Bond et al., 2007; Cauchoix, Hermer, Chaine, & Morand-Ferron, 2017). The behavioural flexibility is then measured by comparing the values of the reversal with the values of the original acquisition (Rayburn-Reeves et al., 2013). In serial reversal learning (SRL) paradigms, sometimes also termed as "successive discrimination reversal" (North, 1950) or "habit reversal" (Bitterman, 1965), this alternating

discrimination training with the same stimuli and switching of reinforcement is repeated in a long series again and again (Shettleworth, 1998, 2010).

When applying this paradigm, an experimental subject typically needs extended time for adapting to the first reversals, but the more successive reversals it has experienced, the faster it reaches the intended goal (Krechevsky, 1932; Nissen, Riesen, & Nowlis, 1938; Sutherland & Mackintosh, 1971). The characteristic error pattern for successive reversals shows an initial increase, followed by a progressive decline of errors (Bitterman, 1965; Gossette, 1968; Shettleworth, 1998, 2010). As growing experience facilitates the learning of later reversals (Shettleworth, 1998, 2010), it will take a more flexible individual a shorter time and/or fewer trials to start reacting to the changed contingencies. Buytendjike (1930) termed this effect as “learning-to-relearn”, and Barrows (2011) describes this phenomenon as a form of generalisation. Harlow (1949) referred the expression “learning-to-learn” specifically to the performance enhancement in his learning set tasks. In this kind of discrimination problems, instead of the reward contingencies, the presented stimuli are changed from one problem (here: reversal) to the next (Delius & Delius, 2012; Mackintosh, 1974). Thus, the inter-reversal improvement (i.e. from one reversal to the next) in SRL tasks might be explained in terms of this aforementioned effect (Shettleworth, 1998, 2010; Thompson, 1957). Another explanation for such kind of improvement, but also for that throughout a reversal (i.e. intra-reversal improvement), would be the use of a “win-stay, loose-shift” strategy: choose the just rewarded stimulus again and again as long as it is rewarded and when it is not rewarded anymore, switch to the other stimulus (Levine, 1959, 1965; Shettleworth, 1998, 2010). An ideal application of this rule would be a one-trial reversal (Davey, 1989), where an individual completes the whole reversal with a single error as it has been shown repeatedly in rats (e.g. Buytendijk, 1930; Dufort, Guttman, & Kimble, 1954; Mackintosh, Mcgonigle, & Holgate, 1968; Mackintosh, Wilson, & Boakes, 1985; North, 1959) and primates (e.g. Nissen et al., 1938; Schusterman, 1962).

Initially, test subjects were prepared with discrimination problems like those used in RL for sensory capacity studies. Only later this method was utilised for investigating the process of learning itself (Spence, 1936). With SRL paradigms the learning capacities of highly diverse animals have been tested during the 50s, 60s and 70s of the last century.

Table 1, at the next page, provides a rough overview of the wide range of tested species.

Table 1 - Examples of the various animals tested: Species, publication year and, authors. Sorted in non-vertebrates, vertebrates and primates.

	SPECIES	YEAR	AUTHOR(S)
NON-VERTEBRATES	Octopuses	1958	Boycott & Young
	Cockroaches	1964	Longo
	Crabs	1960	Datta, Milstein, & Bitterman
VERTEBRATES	Newts	1949	Seidman
	Fish	1958	Bitterman, Wodinsky, & Candland
		1960	Warren
		1967	Gonzalez, Behrend, & Bitterman
	Terrapins	1949	Seidman
	Turtles	1966	Holmes & Bitterman
	Chickens	1960	Warren, Brookshire, Ball, & Reynolds
	Pigeons	1962	Bullock & Bitterman
		1966	Gonzalez, Berger, & Bitterman
		1967	Gonzalez, Behrend, & Bitterman
		1968	Gossette
		1971	Williams
	Bats	1971	Ellins & Masterson
	Cacomistles	1968	Gossette, Kraus, & Speiss
	Cats	1960	Cronholm, Warren, & Hara
		1966	Warren
	Coatimundis	1968	Gossette, Kraus, & Speiss
	Horses	1962	Warren & Warren
	Kinkajous	1968	Gossette, Kraus, & Speiss
	Raccons	1962	Warren & Warren
		1968	Gossette, Kraus, & Speiss
	Rats	1932	Krechevsky
		1950	North
		1952	Gatling
		1968	Mackintosh, Mcgonigle, & Holgate
		1969	Mackintosh & Little
	Skunks	1968	Gossette, Kraus, & Speiss
Primates	Capuchins	1968	Gossette, Kraus, & Speiss
	Gibbons	1971	Rumbaugh
	Gorillas	1971	Rumbaugh
	Rhesus monkeys	1966	Warren
	Squirrel monkeys	1968	Gossette, Kraus, & Speiss
	Talapoins	1971	Rumbaugh

Initially, the differing success in RL tasks between tested species was thought to possibly mirror an underlying evolutionary progress (Kendler, 1959). There were attempts of using the results of such learning experiments to compare the tested animals´ improvement and interpret it in terms of building an evolutionary rank-order of intellectual progress (Warren, 1965). The idea of a "*scala naturae*", a linear progress from less towards higher complexity-levels in living beings, with humans on top of it (Hodos & Campbell, 1969; Shettleworth, 1998, 2010), dates back to Aristotle (Archibald, 2015). During Darwin´s time, this scale of improvement in nature was transformed to a "phylogenetic scale" of cognition, where brain evolution is assumed as a continuum of unilinear complexity-enhancement (Striedter, 2005). Not until last century´s 40s and 50s his discovery of the branched speciation ('Corals of Life') replaced the up until then popularly accepted linear progress of evolution (Striedter, 2005).

The direct comparison of various experiments can cause problems: e.g. the usage of different stimuli, and, moreover, the comparison of only distantly related species is tricky, since the tested animals might differ in their motivational, as well as perceptual and motor abilities (Mackintosh et al., 1985; Mills, 2010). A promising approach for testing models of cognitive evolution and avoiding problematic differences between the compared species, as Mackintosh and colleagues (1985) pointed out, is the comparative method where close relatives are tested (Harvey & Pagel, 1991). Birds seem to be a promising group for this kind of comparison (Mackintosh et al., 1985) and Clayton & Emery (2015) specifically suggest corvids and parrots as suitable models to explain the evolution of human cognition. Therefore, this study concentrates on the avian class.

Many SRL studies with birds have a physiological focus, in order to determine differences and similarities between avian and mammalian brain functions. Some examples are: the lateralisation of RL in pigeons (Diekamp, Prior, & Güntürkün, 1999), the influence of lesion (Hartmann & Güntürkün, 1998; Shimizu & Hodos, 1989) or blocked receptors (Diekamp, Kalt, Ruhm, Koch, & Güntürkün, 2000; Lissek, Diekamp, & Güntürkün, 2002) in certain avian brain parts. Others are more of the methodological kind: e.g. one group tested and proved the superiority of real objects over artificial images in keas (*Nestor notabilis*) (O'Hara, Huber, & Gajdon, 2015), and another the influence of the criterion level during RL in two parrot species (*Diopsittaca nobilis* and *Pionites melanocephala*) (van Horik & Emery, 2018).

Bond and colleagues (2007) compared the SRL performance of three corvid species (*Gymnorhinus cyanocephalus*, *Nucifraga columbiana* and *Aphelocoma californica*), where the authors suggested that the tested species' behavioural flexibility is mostly influenced by the social makeup they live in. A study with two species of Darwin's finches (*Cactospiza pallida* and *Camarhynchus parvulus*) indicated a possible relationship between neophobia and flexible behaviour (Tebbich, Stankewitz, & Teschke, 2012).

1.3 Why Corvids?

The behavioural adjustment to local challenges via individual experiences is enabled by learning (Barrows, 2011; Shettleworth, 1998, 2010). It is a precondition for intelligence (Herrmann, 2016), which in turn is a kind of adaptation process (Piaget, 1952). One avian family has been shown to be exceedingly intelligent: namely corvids (Clayton & Emery, 2005; Emery & Clayton, 2004; Taylor, 2014).

For a long time, the behaviour of birds was assumed of being instinct driven and inflexible because of a wrong notion about how the avian brain is organised (Reiner, 1986; Roth, 2013). However, recent years' insights into vertebrate brain evolution changed the view of a consecutive adding of new parts (Striedter, 2005). Indeed the forebrains of mammals and birds differ substantially: the mammalian pallium is organised in layers, whereas the avian pallium consists of nuclei (Güntürkün, 2005, 2012). But, both classes have a similar cortical structure which serves the same cognitive operations (Güntürkün, 2012; Güntürkün & Durstewitz, 2001). In addition, despite their smaller brain size, and because of higher neuronal densities in the forebrain, songbirds and parrots possess at least similar neuron numbers as primates do (Olkowicz et al., 2016). And also, as Roth (2013) pointed out, neither the absolute nor the relative brain size are useable factors for the comparison between species, especially because only certain brain parts are responsible for intelligence. Instead the number of neurons in these parts, the wiring among them and their processing speed could serve this purpose (Roth, 2013; Roth & Dicke, 2005).

Owing to similarities in anatomy, cognition, neurochemistry and electrophysiology (Emery, 2006; Güntürkün, 2005) the avian neostriatum caudolaterale (NCL) is suggested to be the functional equivalent to the mammalian prefrontal cortex (PFC) (Güntürkün, 2005; Mogensen & Divac, 1982). As Shettleworth (1998, 2010) emphasised, every species is

equipped with particular abilities of working out their ecologically relevant challenges. Based on a similar selection pressure, both, birds and mammals, developed and evolved convergently alike cognitive skills for problem solving (Güntürkün, 2005, 2012), and mental flexibility (van Horik & Emery, 2018). Particularly corvids, parrots and apes face comparable survival challenges (Emery, 2006; Emery & Clayton, 2004). Since the avian NCL and the mammalian PFC serve similar cognitive operations, Herculano-Houzel (2017) proposed the possibility of a direct neuron number comparison between these two structures.

1.4 Study Species

The azure-winged magpie (*Cyanopica cyanus*) is a social living member of the Corvidae family (Brooks, Dunn, & Cramp, 1994). Breeding gregariously in colonies, and having helpers at the nest (Madge, 2009), this species shows proactive prosociality (Horn, Scheer, Bugnyar, & Massen, 2016). It is resident in eastern Asia and has only lately been recognised as a disjoined species from the Iberian magpie (*Cyanopica cooky*) (del Hoyo & Collar, 2016). It occurs in diverse habitats from open woodland over cultivated land with groves and scrubs to grassland (Brooks et al., 1994). Azure-winged magpies are omnivorous and feed on invertebrates as well as fruits and nuts, and furthermore they cache redundant food (Madge, 2009). In captivity these birds can reach a maximum age of up to 14 years (Grummt & Strehlow, 2009). These socio-ecological factors make this species a suitable subject for testing cognitive flexibility (Emery, 2006).

Figure 1 - Azure-winged magpie (*Cyanopica cyana*): Rey.

The birds, which were used for this thesis, are captive individuals. However, Cauchoix and colleagues (2017), were able to show that great tits (*Parus major*) achieve both in the wild as well as in captivity a performance improvement in a RL task. Similarly, the collected SRL results of a study conducted in the laboratory could be tantamount to outcomes of an experiment carried out in nature.

The research project, this thesis is part of, also uses SRL for a comparative approach, as it has been done in the past, but this time the compared species are members of one class, namely birds, and were chosen in respect of their brains size and the neuron number at the basis of Olkowicz et al. (2016). The different avian species are tested under almost identical conditions, in order to facilitate a direct performance comparison.

As Emery (2016) put it, such kinds of comparison should not constitute a intelligence competition between animals, but to detect the similarities as well as differences in these species' learning and cognitive abilities. In this way, it might be possible to infer how those differences could be related to the differing brain structures of these species (Emery, 2016).

1.5 Hypothesis & Aims

In this thesis, I examined whether azure-winged magpies improve their performance over a course of 15 successive colour reversals. The aim was to analyse how long the individuals would need to learn the reversals, and whether the animals could "learn-to-relearn". According to Olkowicz and colleagues (2016) the brain of a azure-winged magpie has 741 million neurons, with 400 million neurons in the pallium, and a weight of 3.39 g. These numbers compare well in relation to the brains of other songbirds: e.g. the hill mynah (*Gracula religiosa*) with 906 million neurons in total, including 410 pallial neurons and a brain weight of 3.67 g, or the starling (*Sturnus vulgaris*) with 483 million total neurons, 226 million neurons in the pallium and a brain weight of 1.86 g (Olkowicz et al., 2016), and mammals: e.g. the tree shrew (*Tupaia glis*) with 261 million total neurons and a brain weight of 2.75 g (Herculano-Houzel, Collins, Wong, & Kaas, 2007), or the guinea pig (*Cavia porcellus*) with 240 million total neurons and a brain weight of 3.8g (Herculano-Houzel, Mota, & Lent, 2006).

I expected, that the tested birds would have most troubles following the first few reversals, however, they should improve their performance with growing experience (Bitterman, 1965; Gossette, 1968; Shettleworth, 1998, 2010). Therefore, the animals were

presumed to decrease their needed trials and thereby the amount of errors, together with the needed time (Bond et al., 2007) over the 15 reversals. Due to the distinct ability of avian colour vision (Emery, 2016; Varela, Palacios, & Goldsmith, 1993), the birds should have no problems in distinguishing the two presented stimuli.

2 MATERIALS & METHODS

2.1 Abbreviations

Throughout this master´s thesis some abbreviations are used repeatedly. Table 2 offers a collection of these, together with the term they stand for and a short definition.

Table 2 - Abbreviations: the occurring abbreviations, as well as the written-out term and a short description are listed here.

ABBREVIATION	TERM	DESCRIPTION
CT	**C**orrection **T**rial	= repetition(s) of the last trial, after the animal chose the wrong stimulus - until it chooses S+,
IA	**I**nitial **A**cquisition	= the original associative stimuli discrimination learning,
ITI	**I**nter**t**rial **I**nterval	= time between two consecutive trials (~30 seconds),
LC	**L**earning **C**riterion	= 17 of the last 20 trials correct (i.e. 85%),
R_x	**R**eversal Nr.**X**	= the X^{th} reversal of the IA,
RI	**R**eversal **I**ndex	= ratio of $\frac{1+mean\ TTC\ for\ a\ phase}{1+TTC\ on\ phase\ 0}$,
S+	positive **s**timulus	= rewarded colour,
S-	negative **s**timulus	= not rewarded colour - the choice triggers an ITI,
(S)RL	(**S**erial) **R**eversal **L**earning	= iterated alternation of the reward allocation,
TTC	**T**rials **T**o **C**riterion	= amount of required trials and CTs for reaching the LC,

2.2 Test Subjects

Study subjects were six captive azure-winged magpies (*Cyanopica cyanus*), four females and two males, kept at the Animal Care Facility of the Department of Cognitive Biology of the University of Vienna. All birds were marked individually with coloured leg rings, and at the study onset (in February 2018) the subjects ranged in age from 20 to 32 months (Table 3). The birds were housed together in an outdoor aviary (4.25 x 3.00 x 3.20 m), which could be divided in two equal compartments (A & B, Figure 2) via slide doors. The ground was covered with sand and gravel, and the aviary additionally contained a tree trunk, stones, perches, swinging branches and a birdbath. As protection against rain the aviary´s roof was partially covered, and the main light source was daylight.

The animals were fed once a day with a mixed diet of fresh fruits, berries, vegetables and insects. Furthermore they had ad libitum access to water and dry food ("Beo komplett", NutriBird). Either day-old chicks or boiled eggs with food supplements were provided weekly.

Mealworm (*Tenebrio molitor*) pupas were used for all subjects, except one (Kylo), who received mealworm larvae. The reward-insects were deep-frozen beforehand, in order to kill them, and cut into small pieces to avoid food saturation of the test subjects. The birds were not food-deprived during the test, and the high-quality food reward constituted an additional goody.

The animals, participating in this study, were all naïve to the here applied SRL task, but were used to the close proximity of humans as well as other experimental tasks.

This experiment was approved by the Animal Ethics and Experimentation Board – Faculty of Life Sciences, University of Vienna (No. 2018-022).

Table 3 - Individuals: Names (and abbreviations), colours of identification-rings, sex and hatching moth of the test group.

NAME	RINGS left/right	SEX	YEAR OF HATCHING	PARTNER
Anakin (AK)	silver/blue	♂	June 2015	BB
BB8 (BB)	---/yellow	♀	June 2016	AK
Chewie (CH)	bronze/---	♀	July 2015	KY
Kylo (KY)	---/red	♂	June 2016	CH
Poe (PO)	---/blue	♀	June 2016	---
Rey (RE)	---/green	♀	June 2016	---

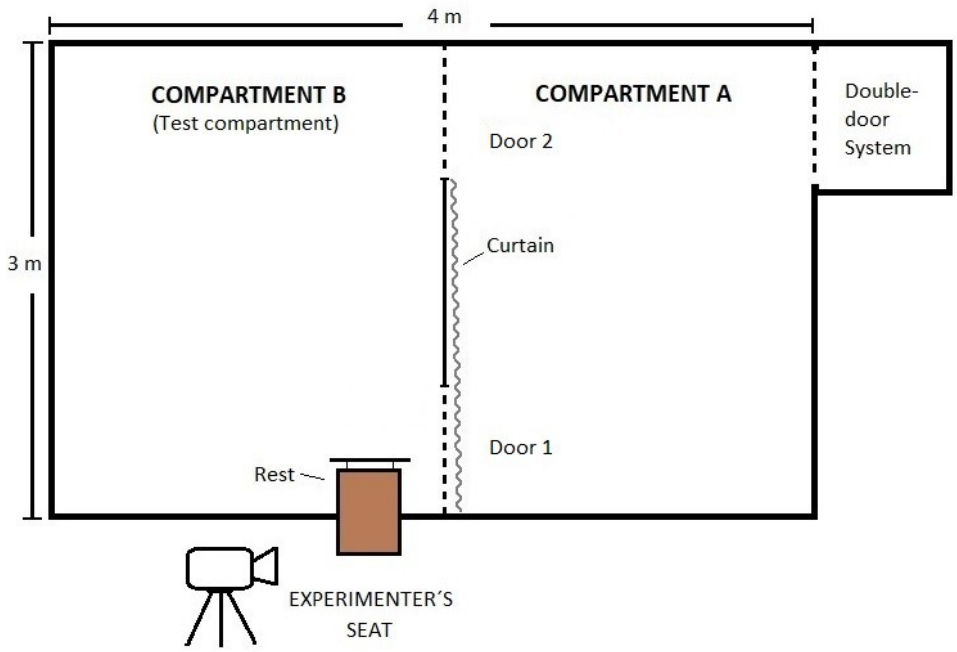

Figure 2 - Aviary Plan: Depicted is the birds' home aviary with the two dividable compartments, the double-door entrance and one part of the experimental setup. Testing took place in compartment B, the rest of the group was in compartment A. To avoid the other birds from observing the experimental task, a curtain was used. The sessions were conducted from outside the aviary, at the experimenter's seat, and filmed by a video camera.

2.3 Apparatus & Stimuli

The apparatus consisted of three parts: I) a sliding board (="sleigh") with II) the two movable colour stimuli and III) a fixated board (="rest"), which served as support and guideway for the sleigh.

The rest was made up of a wooden three-ply board (40 x 30 cm and 1.5 cm thickness, Figure 2 & Figure 3, left), and the sleigh was made of beaverboard (23 x 30 cm and 2.5 cm high, Figure 3, middle). At the top of this sleigh two jars of glass (tea-light holder, ~ 3.8 cm inner diameter) were plugged in parallel, serving as reward bowls. Two wooden discs (6 cm diameter, each with an approximately 20 cm long thin wooden rod), in blue (R=79, G=129, B=189) and yellow (R=255, G=192, B=0), were used both as colour-stimuli and removable covers at once (Figure 3, middle & right).

During the experiment, the test subject was physically isolated from its social group into the test compartment (Compartment B - Figure 2). Into this compartment´s wire mesh a small aperture (7 cm x 30 cm in ~ 1m height) was cut, through which the rest was stuck halfway through and durable affixed. The remaining aperture was shut by use of a down

sliding grid (="shift gate", 15 x 45 cm, Figure 3, left and right), which was therefore self-closing. At the inner front side of the rest, a perch for the test individual was attached, so the bird could easily reach the stimuli as well as the hidden reward underneath these covers. Opposite to the test bird, outside of the aviary, sat the experimenter (="experimenter's seat"). Below the rest, a tarpaulin (90 x 40 cm) was attached to the wire mesh as visual cover, to avoid the test individual from observing the sleighs baiting. In order to prevent the rest of the group from watching the test individual, a white opaque cloth-curtain was fitted between the two compartments.

Figure 3 - Apparatus: Left: picture of experimenter's seat, Middle: sleigh with jars and covers, Right: setup ready for testing.

2.4 Habituation to Apparatus & Test Situation

For habituating the birds to the new setup, the apparatus and the curtain were installed in the aviary 10 days before the beginning of this experiment. Then, for another seven days, the birds were rewarded for landing on the rest and following this, the sleigh was introduced to the group. Each pane was baited with deep-frozen mealworms as well as pupas, and the sleigh was shifted through the gate repeatedly, until all birds approached the apparatus and ate from it without hesitation. The next step focussed on the habituation of the birds to the closing of the two slide doors, as well as the individual isolation. The process was started by stepwise closing door 1 (Figure 2), until the birds got habituated to this movement and to the door being closed for some time. Following this, the habituation process was continued in an analogous manner for door 2 and the curtain. After one week of aforementioned

habituation procedure, no bird showed any signs of distress while both doors and the visual barrier were closed.

Ensuing, the training for separating the individuals proceeded. To do so, door 1 was closed first, and while standing in door 2, a bird was enticed with mealworms to move into the test compartment (Comp. B). As soon as one individual was alone in compartment B, the second door was closed, and the bird got another worm as reward. Then, the curtain was pulled shut and strapped to the wire-mesh, the experimentalist left the aviary and went to the experimenter's seat. From there the shift gate was operated a few times while the bird was rewarded repeatedly with meal worms, and reunited with its group after several minutes. Subsequently, all individuals received some worms, and the separation of another bird started. After 5 weeks (± some days) in total, all individuals were ready to start with the experiment. The coloured covers, serving as stimuli, were only introduced with the first session. If an individual needed re-habituation (i.e. showing unwillingness to approach the assembled sleigh), the habituation to the baited sleigh without stimuli was repeated.

2.5 General Procedure

The data collection was conducted between May and October 2018 in the birds´ home range aviary. Testing took place in sessions from Monday till Friday between 10:30 in the morning and 17:30 in the afternoon. The subjects received not more than one session per day and depending on the individual's motivation, weather conditions and other inalterable variables these sessions lasted between 10 and 60 minutes. Each bird was tested three times a week at least, and needed approximately three and a half sessions on average (± 2 sessions) to finish a reversal.

For the experiment, subjects needed to be separated from the group with the beforehand delineated procedure. After the successful isolation of the test bird, the experimenter left to the test position outside the aviary, started the camera and began with the testing. Out of the test subject's view, the sleigh was baited, and the jars got covered with the coloured discs. After this, the trial started in the following way: the assembled sleigh was placed at the rest and slid through the upheld shift gate, which was closed again immediately. Then the subject had to choose between the two simultaneously presented colour-stimuli (i.e. blue & yellow). By use of the attached rods it was possible for the experimentalist, to make the subjects' reward accessible through pulling the chosen disc backwards. This, however, was only necessary at the study onset, because in later sessions the experienced test birds

opened the jars by themselves by pushing the covers. If the rewarded colour (S+) was picked by the subject, it received the reward, the sleigh was removed from the board, and the trial ended. In a, for the test subject, not visible position re-baiting of the sleigh was performed, and the session continued with the next trial. After a wrong choice (subject picked S-) it received no reward, and the sleigh was removed, but only kept out of the subject's sight for approximately 30 seconds (i.e. inter-trial interval, ITI). Following this, the experimenter presented the sleigh again, using the same colour configuration (i.e. correction trial, CT), for as many correction trials as necessary until the subject chose S+. As soon as the bird made the correct choice, the session proceeded with the following regular test trial.

If a bird did not approach the apparatus for more than five minutes during a trial, the shift-gate was operated several times in order to attract the individual's attention. If this did not work, the sleigh was removed from the rest for approximately 10 seconds and then returned again. After 15 minutes without the subject's participation, this session was aborted, the current trial judged as a CT and the bird was reunited with the rest of the group. The reversal proceeded the following day, starting with the same colour-configuration as it stopped the day before. At the end of a test day, the sleigh and the covers were removed, and the shift gate was locked with a padlock.

All learning tests were conducted by the same experimenter and throughout the session sunglasses were worn to avoid vision cues. The daily sequence of the test-subjects was pseudorandomised.

2.5.1 Initial Acquisition, Serial Reversals & Learning Criterion

For each subject the experiment consisted of two phases: the initial acquisition (IA), which constituted the associative learning of a colour-reward discrimination, and then 15 serial reversals (R) of the original IA. The learning criterion (LC) was defined as follows: 17 out of the most recent 20 trials needed to be correct (i.e. a performance criterion of 85%).

For the IA the rewarded colour (S+) was counterbalanced across subjects: that colour, the test individual approached first in the initial session, was decided to be its S+ for IA (start colour of the individuals – Table 5). As soon as a bird reached LC, the ongoing session ended and the reversal began with the following day's session. Consequently the previous S+ got S- in the next trials, and the former S- was the new S+ (i.e. when an individual started with blue as correct colour, in its first reversal yellow was rewarded, in its second reversal blue was again correct and so on). In order to prevent the animals from adopting a side strategy, the

S+ position (left or right) was pseudorandomised for each trial a priori with an equal number on each side in a 20-trial-block. Furthermore the same stimulus was never presented on the same side for more than two successive trials (except in the case of CTs).

2.5.2 Data Recording

The position of S+ for each animal and reversal was decided in advance and registered in the protocol. Needed CTs were also noted during the session in a tally chart and totalled up afterwards. Raw data were transferred to an Excel-sheet once a week. Additionally every session was video recorded (with a camcorder, Canon Legria HF G25, on a tripod, placed outside the aviary) for further analyses.

2.6 Data Scoring & Analysis

Once an individual reached the LC, its needed trials were summed up over the required sessions for that reversal. The same was done with the needed CTs (= errors). The required time for finishing a reversal was gained from the video records: the time from the beginning of each session's first trial to the ending of the last was clocked, and totalled up for the particular sessions. These are the three measurements evaluated for the analysis.

For a better comparability IA and the 15 reversals were divided into four phases: Phase 0 = IA, Phase I = R_1-R_5, Phase II = R_6-R_{10} and Phase III = R_{11}-R_{15}. For phases I-III the median was computed and additionally the reversal index (RI) was measured. This index is deemed a measurement of RL severity (Rajalakshmi & Jeeves, 1965), and was calculated as the ratio of $\frac{1+mean\ TTC\ of\ a\ phase}{1+TTC\ on\ phase\ 0}$.

All statistical tests were performed with R 3.5.2 (R Core Team, 2018) software. The level of statistical significance (α) was set at 0.05.

For comparing the performance change from IA to R1 the One-sample Wilcoxon signed-rank test was conducted. The Friedman-test was used in order to determine whether there are performance differences between the three phases (Phase I, II, and III). To ascertain which phases are different from the others, the One-sample Wilcoxon signed-rank test was deployed as a post hoc test. Additionally, the Holm-Bonferroni correction was performed, in order to take the multiple comparisons into account and adjust the obtained p-values.

To detect whether and to what extent the three measures (time, trials & errors) are associated, the Spearman rank correlation coefficient (r_s) was calculated between them.

3 RESULTS

3.1 Was there a performance change from IA to R_1 & did the birds learn?

There was a significant change in performance from IA to R_1 for total errors, i.e. they increased in R_1 (Wilcoxon signed rank, V=0, n=6, p=0.036). Furthermore, there was a tendency of the changes for needed time (Wilcoxon signed rank, V=1, n=6, p=0.059) and total trials (Wilcoxon signed rank, V=1, n=6, p=0.058).

The Friedman-test for determining whether there are performance differences between the four phases revealed significant variation for all three measurements: the needed trials (χ^2=9.4, df=3, n=6 p=0.024, Figure 4), the needed times (χ^2=9, df=3, n=6, p=0.029, Figure 5), and the conducted errors (χ^2=9, df=3, n=6, p=0.02929, Figure 6).

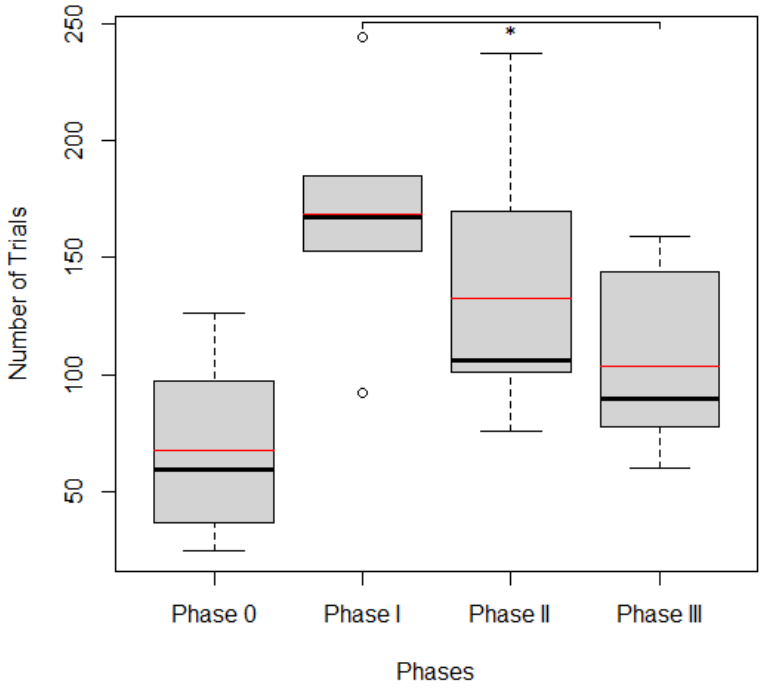

Figure 4 - Total needed trials for each of the four phases: The upper and lower ends of the boxes indicate the 1st and 3rd quartiles (i.e. the 25th and 75th percentile) of the plotted data. The inter-quartile ranges are represented by the boxes length. The dark lines therein denote the median and the red lines the mean. The whiskers extending from the boxes indicate the range of the data. Values more than 1.5 times the inter-quartile range apart from a box are represented as circles and show outlying values. An asterisk indicates significant differences with p<0.05 between Phases I - III.

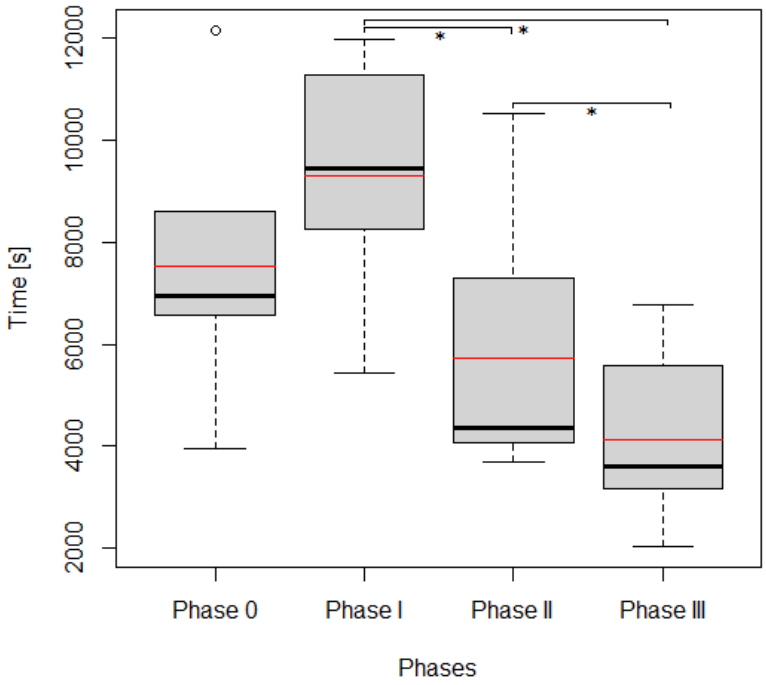

Figure 5 - Total needed time for each of the four phases: The upper and lower ends of the boxes indicate the 1st and 3rd quartiles (i.e. the 25th and 75th percentile) of the plotted data. The inter-quartile ranges are represented by the boxes length. The dark lines therein denote the median and the red lines the mean. The whiskers extending from the boxes indicate the range of the data. Values more than 1.5 times the inter-quartile range apart from a box are represented as circles and show outlying values. An asterisk indicates significant differences with $p<0.05$ between Phases I - III.

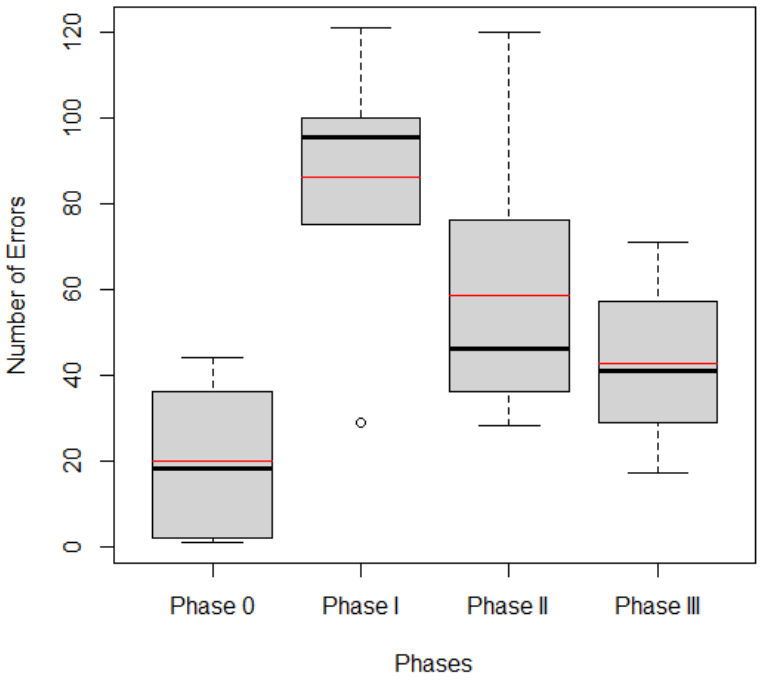

Figure 6 - Total conducted errors for each of the four phases: The upper and lower ends of the boxes indicate the 1st and 3rd quartiles (i.e. the 25th and 75th percentile) of the plotted data. The inter-quartile ranges are represented by the boxes length. The dark lines therein denote the median and the red lines the mean. The whiskers extending from the boxes indicate the range of the data. Values more than 1.5 times the inter-quartile range apart from a box are represented as circles and show outlying values.

To ascertain which phases (Phase I - III) are different from the others, the One-sample Wilcoxon signed-rank was conducted as a post-hoc test. The trials showed a significant difference between phase I and III (Wilcoxon signed-rank, V=21, n=6, p=0.036). In the measurement of times phases I, II and III were significantly different from each other (Wilcoxon signed-rank, V=21, n=6, p=0.036). Whereas, no significanct difference could be observed for errors: neither between phase I and II (Wilcoxon signed-rank, V=17.5, n=6, p=0.171), nor between phase II and III (Wilcoxon signed-rank, V=19.5, n=6, p=0.074). Between phase I and III (Wilcoxon signed-rank, V=20, n=6; p=0.059) a trend was detectable. Following the p-adjustment using the Holm-Bonferroni method, all differences were no longer significant. The raw as well as the adjusted p-values are pooled in Table 4.

Table 4 - Raw and with Holm-Bonferroni correction adjusted p-values for all three measurements: The significant values are in bold and marked with an asterisk.

	Compared Phases	Raw p-value	Adjusted p-value
TRIALS	Phase I/Phase II	0.295	0.295
	Phase I/Phase III	**0.036***	0.108
	Phase II/Phase III	0.093	0.187
TIMES	Phase I/Phase II	**0.036***	0.108
	Phase I/Phase III	**0.036***	0.108
	Phase II/Phase III	**0.036***	0.108
ERRORS	Phase I/Phase II	0.171	0.177
	Phase I/Phase III	0.059	0.177
	Phase II/Phase III	0.074	0.177

3.2 Are there correlations between time, trials & errors?

The Spearman rank correlation yielded a high correlation for total trials and total CTs (Spearman´s rho, r_s=0.860, n=6, p<0.001, Figure 7). The other two measurements also showed a strong relationship: time and total CTs (Spearman´s rho, r_s=0.588, n=6, p= 0.007, Figure 8, left), as well as time and total trials (Spearman´s rho, r_s=0.532, n=6, p= 0.003, Figure 8, right).

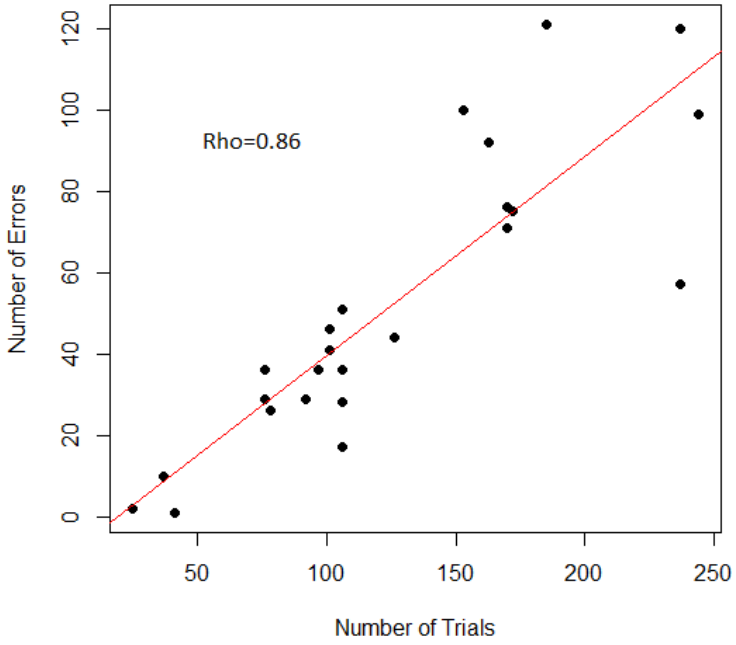

Figure 7 - Correlation between the total needed trials and the total conducted errors: The red regression line shows the marked positive linear relationship between the two measurements.

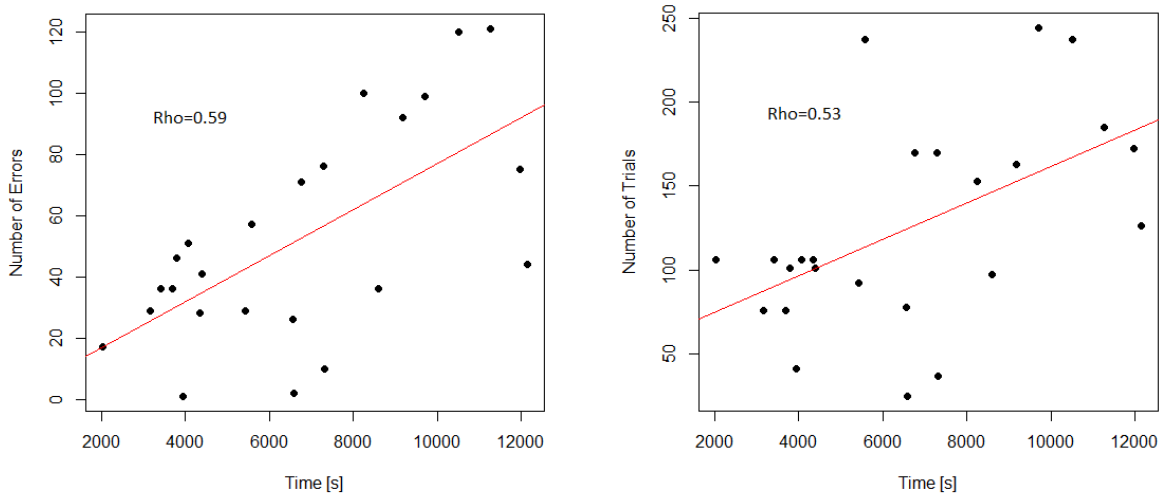

Figure 8 - Correlation between the other two measurements: Left: needed time and total conducted errors. Right: time and total needed trials. The red regression lines show the moderate positive linear relationship for both correlations.

3.3 Which factors might have influenced the results?

Plotting the individual learning curves in one graph, the huge individual differences in performance improvement of the needed trials become visible (Figure 9). Some individuals did not follow the overall pattern (Figures 4-6), but took long to reduce the number of trials (e.g. Kylo) or did not show a constant reduction at all (e.g. Chewie). Only two birds (Anakin and Rey) performed exactly according to prediction and eventually went below their

performance from IA. However, if one looks at the alteration in needed time (Figure 10), all individuals have in common a pronounced initial increase for the required time span of mastering their first, second or third reversal (except for Rey, who needed the most time for her fourth reversal). Sooner or later in the course of this experiment the birds even underwent their first time value, scored in the IA.

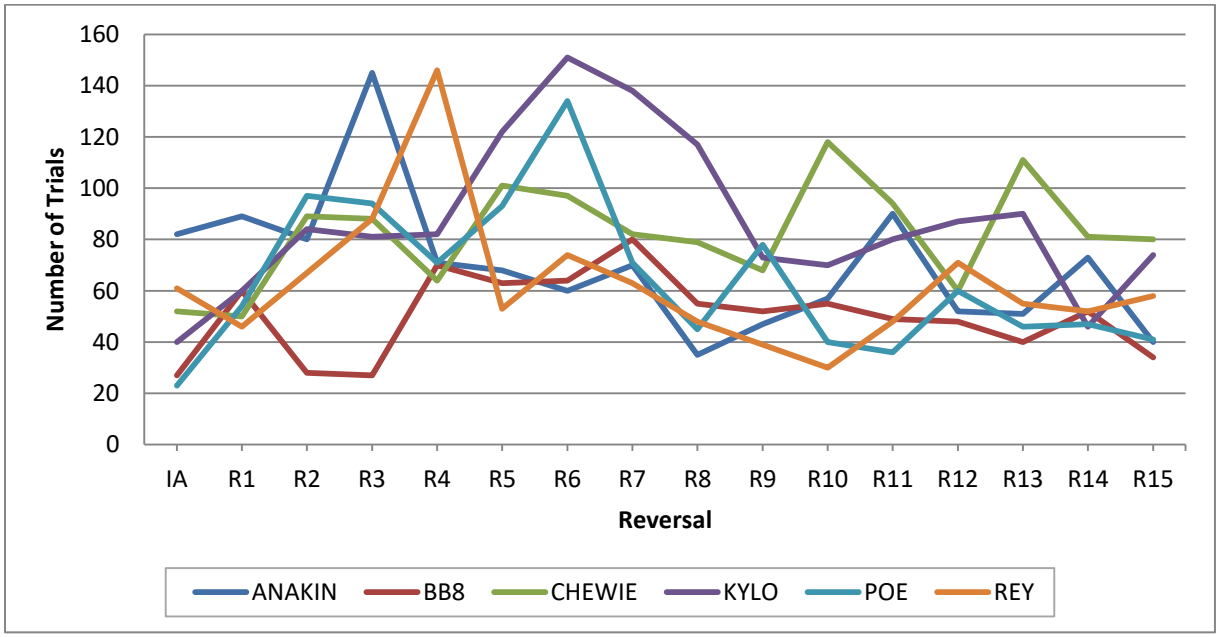

Figure 9 - Regular trials per reversal and for each tested bird: The lines represent the shift in the amount of needed trials over the course of 15 reversals. The different colours indicate the six tested individuals.

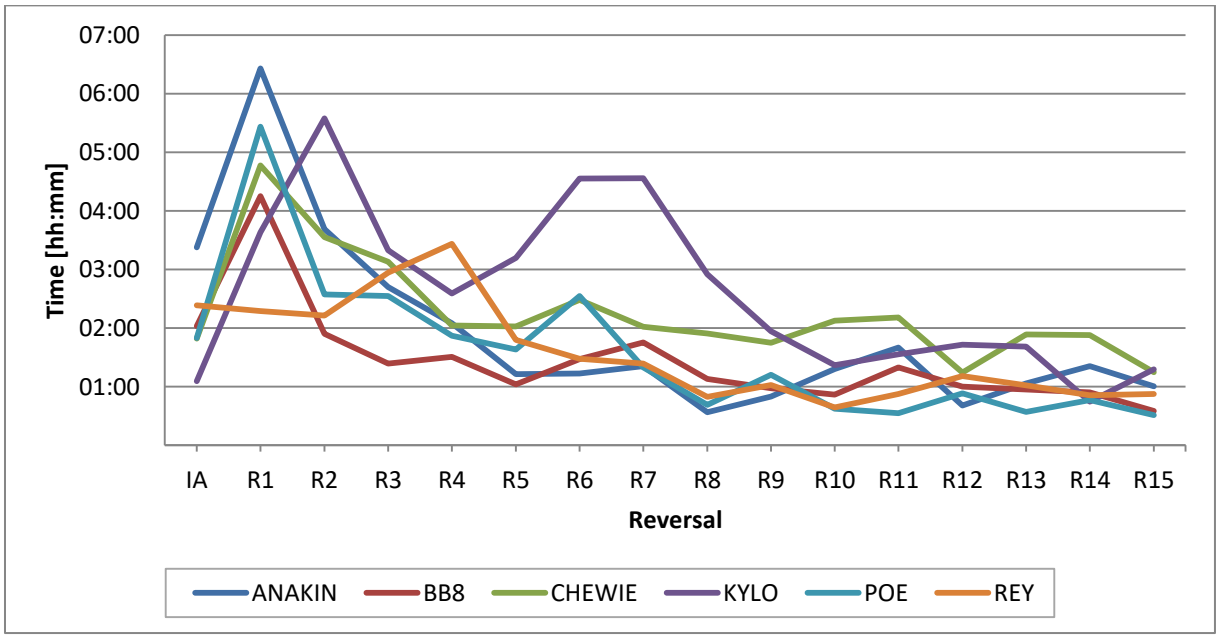

Figure 10 - Time per reversal and for each tested bird: The lines represent the change in the required time span for a reversal over the course of this experiment. The different colours indicate the six tested individuals.

Due to the small sample size (n=6), only exploratory data analysis was possible for the question of other performance influencing factors. To facilitate the visual comparison, the reversal index was used.

The comparison between the RI over the three phases (Table 5) indicates a linear decrease in reversal difficulty from phase I, over phase II, to phase III for three birds (Chewie, Poe and Rey). The remaining three individuals either had most problems in phase II followed by phase I (BB8 and Kylo), or phase I followed by phase III (Anakin).

Table 5 - Reversal indices for all individuals in the three phases, and their sex: The RI is the ratio of the mean number of TTC for the particular phase, divided by the number of TTC during IA (=Phase 0). Colour of the lines code for S+ during IA.

BIRD	SEX	Phase I	Phase II	Phase III
AK	♂	1.68	0.72	0.88
KY	♂	4.01	5.33	3.02
CH	♀	2.48	2.20	1.93
BB	♀	2.55	3.23	2.19
RE	♀	1.84	0.95	0.90
PO	♀	6.91	4.35	2.56

4 DISCUSSION

The aim of this thesis was to investigate the cognitive and thereby behavioural flexibility in azure-winged magpies. The birds' performances in all three measurements (i.e. trials, errors, and time) dropped from the results accomplished during IA, as compared to those achieved in their R_1. Inspecting the performance change from one phase to the next, the birds showed a progressive improvement over the course of the testing period. Moreover, the three measurements were correlated among one another. Considering the individual learning curves for the measure of regular trials per reversal, very pronounced individual differences in performance improvement become visible, whereas the fluctuation of the needed time for the individuals is relatively congruent.

The first findings are in line with my predictions, as the animals had most of the problems during and ensuing the first reversal, but improved their performance in all three measurements with the following reversals. So they learned how to cope with the repeated switching between the reward contingencies during this experiment and might have learned to re-learn in the sense of Buytendijk (1930) and Harlow (1949). However, for the needed trials as well as the conducted errors, the birds did not reach a constant level of the values obtained during the IA, but remained above these values. Only for the measurement of needed times the IA-level was undercut by most individuals. It is possible, nevertheless, that the birds would also have undergone their IA-values of the needed trials and the conducted errors with a prolonged testing-period, as described for example for rats by Krechevsky (1932), and pigeons (Bullock & Bitterman, 1962; Gonzalez, Behrend, & Bitterman, 1967).

On the individual level, the performance of the six tested birds varied strongly. One hypothetical explanation for a large variation in performance between the birds could be the age of the tested individuals. On the one hand, in the course of a lifetime it is expected, that individuals gather experience, which in turn can influence the performance in challenging tasks (Thornton & Lukas, 2012) such as SRL. On the other hand, executive functions, as for example cognitive flexibility, decline at a certain age, this is known for humans (Berry et al., 2016; Haaland, Vranes, Goodwin, & Garry, 1987) and has also been shown in non-human great apes (Manrique & Call, 2015), as well as in different dog breeds (Beagles: Milgram, Head, Weiner, & Thomas, 1994; Border Collies: Wallis et al., 2016). Azure-winged magpies in

captivity can reach an age of up to 14 years (Grummt & Strehlow, 2009). As all my tested birds were around a similar average age (3 ± 0.5 years), the age-related decline of cognitive abilities is an unlikely explanation for the marked individual differences in their performance. Whereas prior experiences, gained in earlier studies, might have helped some birds, the tested individuals were all naïve to the used paradigm.

Another hypothetical factor explaining the variation in performance could be the sex of the tested individuals. Different studies found that the sex (e.g.: Lucon-Xiccato & Bisazza, 2014; Range, Bugnyar, Schlögl, & Kotrschal, 2006; Titulaer, van Oers, & Naguib, 2012), and with that the exposure to or the level of specific hormones (Bebus, Small, Jones, Elderbrock, & Schoech, 2016; Rogers, 1974) of the test individuals can influence their achievements in cognitive tasks. Lucon-Xiccato & Bisazza (2014) were able to show in a colour-discrimination RL study with guppies (*Poecilia reticulata*), that females were more flexible in the first reversals, because males were more persistent in displaying the prior rewarded response. These results were interpreted in relation to the distinct roles, the sexes of guppies (polygamous species) play in reproduction (Lucon-Xiccato & Bisazza, 2014). However, as azure-winged magpies form monogamous pair-bonds (Madge, 2009), the performance differences in a SRL task, should be less distinct between the sexes (Lucon-Xiccato & Bisazza, 2014). Indeed, it is not possible to detect any sex-specific pattern within the RI's in Table 5.

Finally, the observed individual differences in performance could be related to the individuals' personality'. The term personality refers to a set of consistent behaviours and physiological reactions, which is also denoted as coping style (Koolhaas et al., 1999), profile (Groothuis & Carere, 2005) animal temperament (Réale, Reader, Sol, McDougall, & Dingemanse, 2007), behavioural type (Sih, Bell, & Johnson, 2004; Sih & del Giudice, 2012), as well as predisposition, or individuality (Carere & Locurto, 2011). These alternative reaction patterns for challenge responses are constant over time and between situations, but vary between individuals (Coppens, de Boer, & Koolhaas, 2010; Koolhaas et al., 1999; Wolf & Weissing, 2012).

Range et al. (2006) found sex-dependent differences in learning a discrimination task in ravens (*Corvus corax*). The authors explained those in terms of a possible connection between an individuals´ performance in a learning test and their personality (Range et al., 2006). Furthermore, Carere & Locurto (2011) proposed an possible influence of the personality type on cognition, and, additionally, that distinct personalities could react in a

divergent manner to similar situations (Carere & Locurto, 2011). For wild cavies (*Cavia aperea*) a connection between personality and learning as well as behavioural flexibility could be found (Guenther, Brust, Dersen, & Trillmich, 2014), and also in bank voles (*Myodes glareolus*) a relationship between individual behaviour, rate of learning and flexibility was shown (Mazza, Eccard, Zaccaroni, Jacob, & Dammhahn, 2018). In zebra finches (*Taeniopygia guttata*) Brust et al. (2013) were able find a link between personality and cognitive abilities too.

In the current study, the distinct individual differences between the tested azure-winged magpies were apparent over a series of reversals, hinting towards temporal consistency and thus personality. Since the personality concept is independent from the individuals' age and sex (Carere & Locurto, 2011; Groothuis & Carere, 2005), this explanatory approach might be the most convincing.

Note that personality can also constrain an individuals' behavioural flexibility and might cause the exhibition of suboptimal behaviour (Sih et al., 2004). Therefore, Dingemanse and colleagues (2010) stress the importance of an integrative approach to the study of animal personality and individual behavioural flexibility, especially, because of the possibility of an co-evolution from personality and cognition (Carere & Locurto, 2011).

Consequently, for follow up studies, it would be interesting to test more individuals, over a longer period (i.e. more reversals) and, especially, integrate tests for personality, in order to answer the question to what extent behavioural types functionally influence the individual performance on cognitive tasks.

As this study on azure-winged magpies is part of a big comparative project involving > 20 species, the performance of these birds will be eventually compared with those of other corvids, parrots, pigeons, chickens, tinamous and ostriches, all tested with the same procedure and in a similar setting.

ABSTRACT

How flexibly animals respond to environmental changes may vary highly between species. One paradigm to test for behavioural flexibility is serial reversal learning (SRL), where individuals first learn to distinguish between two presented stimuli, from which only one leads to the reward. Consequently, the subjects develop a preference for this S+, and following this, the reward contingencies are reversed (i.e. the former S- gets rewarded instead). Thus, the individuals have to relearn the altered association and develop a new preference. This contingency alternation can be repeated several times, and the individuals' ability in adapting to this procedure can be measured in terms of needed trials, error rates and time to acquisition per reversal.

The described paradigm was used to investigate the performance improvement of a highly social corvid species, the azure-winged magpie (*Cyanopica cyanus*). The animals (4 ♀, 2 ♂) were trained on a visual binary-choice discrimination problem (blue vs. yellow), over the course of 15 reversals. The prediction was, that the birds should ´learn-to-(re-)learn´, i.e. improve their error rates and acquisition time over the successive reversals.

The results generally supported the prediction of a gradual improvement in performance, although, the animals exhibited pronounced individual differences in their progress. Among other factors, personality characteristics are discussed as a possible reason for the unexpectedly large individual variation in performance.

ZUSAMMENFASSUNG

Die Flexibilität mit der Tiere auf Veränderungen in ihrer Umwelt reagieren, ist von Art zu Art unterschiedlich stark ausgeprägt. Ein experimenteller Ansatz diese Flexibilität im Verhalten zu testen ist Serial Reversal Learning (SRL). Dabei lernt ein Test-Subjekt zuerst zwischen zwei Reizen zu wählen, von denen jedoch bloß einer belohnt wird. Sobald dieser S+ bevorzugt von dem Subjekt gewählt wird, wird die Belohnungs-Zuordnung umgekehrt, und die Wahl von S- wird belohnt (=Reversal). Somit muss das Subjekt eine neue Reiz-Belohnung-Verknüpfung lernen und eine neue Präferenz bilden. Dieser Belohnungs-Wechsel zwischen den Reizen kann wiederholt durchgeführt werden. Die Anpassungsfähigkeit des Test-Subjekts an diese Reversals kann man dann über die jeweils benötigten Durchgänge, die Fehleranzahl und die benötigte Zeit messen.

Für diese Masterarbeit wurden Blauelstern (*Cyanopica cyanus*), sozial lebende Rabenvögel, mit dem beschriebenen Ansatz getestet. Die Tiere (4 ♀, 2 ♂) lernten die Unterscheidung von zwei Farb-Reizen (Blau & Gelb) und wurden mit 15 Reversals konfrontiert. Es wurde angenommen, dass die Vögel im Laufe des Experiments ihre Leistung verbessern würden, indem sie sowohl die Fehleranzahl als auch die benötigte Zeit reduzieren würden.

Die Ergebnisse bestätigten die Vermutung einer schrittweisen Leistungsverbesserung, allerdings zeigten die Tiere ausgeprägte individuelle Unterschiede in ihrem jeweiligen Fortschritt. Diese Erkenntnisse werden im Bezug auf mögliche Gründe für diese individuellen Differenzen diskutiert, und laufen auf den möglichen Einfluss der zugrundeliegenden Persönlichkeit der Tiere auf deren Erfolg hinaus.

FIGURE & TABLE INDEX

All photographs were taken by the author.

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