Learning and motor-impulse control in crows and domestic chickens

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Abstract

Cognitive abilities allow animals to navigate through complex, fluctuating environments. Examples include behavioural flexibility, which is the ability of an animal to alter their behaviour in response to a novel stimulus and behavioural inhibition, defined as the ability to control a response in order to choose a conflicting course of action. Behavioural flexibility and inhibitory control are expected to vary between and within species based on socio-ecological factors. In the present study we tested performance of a captive group of eight (seven carrion and one hooded) crows (from now-on crows), *Corvus corone,* and ten domestic chickens, *Gallus gallus domesticus*, in two cognitive tasks. The cylinder task was used as a test of motor inhibitory control, and reversal learning as a measure of learning ability and behavioural flexibility. Four crows and nine chickens completed the cylinder task, eight crows completed the reversal learning experiment and nine chickens were tested in the acquisition phase, however three chickens did not complete the reversal phase of the experiment due to time constraints. Crows performed better in the cylinder task (73 % correct trials) compared to domestic chickens (23 % correct trials). In the reversal learning experiment, species did not significantly differ in the number of trials until learning criterion was reached. In crows, individuals who needed fewer trials to reach learning criterion in the acquisition phase also needed fewer trials to reach the criterion in the reversal phase. This relationship was lacking in domestic chickens. Performance in the learning task did not correlate with performance in the cylinder task in domestic chickens. Our results suggest crows to possess better motor-inhibitory control compared to domestic chickens. In contrast learning performance in a reversal learning task did not differ between crows and domestic chickens, indicating similar levels of behavioural flexibility in both species. Interestingly, we describe notable individual differences in performance in both species. We stress the importance not only to compare

cognitive performance between species but also within individuals of the same species when investigating the evolution of cognitive skills.

Key words: carrion crows, domestic chickens, inhibitory control, motor inhibition, reversal learning,

Introduction

Cognitive abilities allow animals to navigate through complex, fluctuating environments (Budaev et al., 2019) and critically affect survival and fitness of individuals (Shettleworth, 2009). Examples of cognitive abilities include behavioural flexibility, an animals' ability to alter their behaviour in response to a novel stimulus and to modify responses to familiar stimuli or the inhibition of previously successful behavioural strategies. A common test of behavioural flexibility is the reversal learning task, where an individual has to learn a discrimination task (acquisition phase) and subsequently must respond to the previously unrewarded stimulus (reversal phase; (Izquierdo et al., 2017)).

Behavioural inhibition is the ability to control a response in order to choose a conflicting course of action (Duque & Stevens, 2017). Environmental uncertainty can negatively affect inhibitory control. Pheasants, *Phasianus colchicus*, for whom a previously learned association between a visual cue and a food reward was perturbed in order to simulate environmental uncertainty, performed worse in an inhibitory control task compared to control individuals (Griffin et al., 2020). A common test of behavioural inhibition is the cylinder task. In this detour task, individuals are trained to take a food reward from an opaque cylinder or tube, which is open at both ends. Once individuals are reliably doing this, the opaque cylinder is replaced by a transparent one. The focal individual's ability to inhibit the motor impulse to try to reach the reward through the long side of the cylinder, which forms a transparent barrier between the individual and the reward, and detour to take the reward from the open ends is assessed (Kabadayi et al., 2018). In recent years, behavioural inhibition performance has been tested in a wide range of species (for example: cognitive flexibility: great tits, *Parus major*: Cauchoix et al. 2017; kea, *Nestor notabilis*:

O'Hara et al. 2015; red-footed tortoise, *Chelonoidis carbonarius*: Bridgeman and Tattersall 2019; inhibitory control: cats, *Felis catus*: Bobrowicz and Osvath 2018; common waxbills, *Estrilda astrild*: Gomes et al. 2020; dogs, *Canis familiaris*: Brucks et al. 2017; goats, *Capra aegagrus hircus*: Langbein 2018; great tits, *Parus major*: Isaksson et al. 2018; guppies, *Poecilia reticulata*: Lucon-Xiccato et al. 2017; sailfin molly, *Poecilia latipinna*: Gibelli et al. 2019; vervet monkeys, *Chlorocebus pygerythrus*: Kumpan et al. 2020). A large-scale study by MacLean et al. (2014) compared inhibitory abilities in 36 species and found a positive correlation between absolute brain size and motor self-regulatory performance. Amongst birds tested, different corvid species (common ravens, *Corvus corax*, New Caledonian crows, *Corvus moneduloides*, and Western jackdaws, *Corvus monedula*) displayed the highest levels of impulse control (Kabadayi et al., 2016). In hyenas, *Crocuta crocuta*, individuals living in larger groups exhibited greater inhibitory control (Johnson-Ulrich & Holekamp, 2020), however inhibitory control was not associated with the ability to innovate (Johnson-Ulrich et al., 2018).

In addition to species differences, cognitive performance in animals also differs between individuals, for example based on sex (Range et al., 2006) or personality (Dougherty & Guillette, 2018). Individual difference in cognitive performance is relatively understudied and only recently the importance to understand causes and consequences of individual variation in cognitive performance has been acknowledged (Boogert et al., 2018). In addition to understanding variation in cognitive performance between species, in order to fully understand the evolution of different cognitive abilities, it is also critical to further investigate temporal (correlations in performance across different times) and contextual (correlations in performance across different tasks) repeatability of performance (Cauchoix et al., 2017).

In the last decades, the cognitive abilities, including behavioural flexibility and inhibitory control, of corvids have been heavily studied (Taylor, 2014; Wascher, 2018). For example, black-billed magpies, *Pica hudsonia,* performed similarly compared to different monkey species in a basic concept learning task (Wright et al., 2017), and jungle crows, *Corvus macrorhynchos*, learned to discriminate shapes and form concepts (Bogale & Sugita, 2014). In a reversal learning task, New Caledonian crows, a tool-using corvid species and carrion crows, a closely related non-tool using species, showed similar performance, suggesting that tool use is not causing enhanced learning performance in crows (Teschke et al., 2013). Corvids paralleled performance of great apes in a motor-inhibition task (common ravens: 100 %; jackdaws: 97 %; New Caledonian crows: 92% success (Kabadayi et al., 2016) and carrion crows as well as common ravens were able to delay gratification in a qualitative, but not quantitative context (Dufour et al., 2012; Hillemann et al., 2014; Wascher et al., 2012).

In contrast to corvids, fewer studies have investigated the cognitive abilities of domestic chickens, *Gallus gallus domesticus.* Inhibitory control in chickens is related to housing conditions. In a study by Ferreira et al. (2020) domestic chickens showed low levels of motor impulse control in the cylinder task (32 % success). Impulse control was further affected by individual ranging habits. Individuals with a higher movement range showed a poorer performance compared to low ranging individuals. In red junglefowl, *Gallus gallus*, cognitive flexibility and exploratory behaviour correlated in an age and sex dependent manner. More explorative chicks showed higher cognitive flexibility compared to less explorative ones, while the opposite association was found for adult females (Zidar et al., 2018). Both groups, corvids and chicken are considered to organise in complex social systems (Garnham & Løvlie, 2018; Wascher, 2018), which is assumed a driving factor in the evolution of cognitive skills (Dunbar, 1998).

In the present study we investigated the performance of crows and domestic chickens in two cognitive tasks, the cylinder task as a test of motor inhibitory control, and reversal learning as a measure of learning ability and behavioural flexibility. In contrast to domestic chickens, crows are widely considered 'brainy' birds (Taylor, 2014), thus we could expect high levels of motor inhibition in crows, but not in chickens. Further, it could be expected that corvids reach learning criterion in the reversal learning task quicker compared to chickens and to show higher behavioural flexibility. We do not necessarily share this expectation and aim to contribute to knowledge about individual performances in cognitive tasks in two well-established model species.

Methods

Subjects and housing

The total study population consisted of eight crows, seven carrion crows, *Corvus corone corone,* and one hooded crow, *Corvus corone cornix*. All crows were tested at the Konrad Lorenz research station (KLF) in Grünau, Austria from October 2010 to August 2012. Crows were held in large outdoor aviaries (15 m^2), in two male-female pairs, one trio (one male, two females) and one single housed individual. Testing was conducted either in the main aviary with one animal visually and spatially separated from the others, or in a separate, spacious testing room, which birds entered voluntarily upon request. Rewards consisted of greaves, *i.e.*, fried pork skin and cheese. All focal individuals were hand-raised between 2007 and 2011, either at the KLF or by private people. Crows were captured and brought into captivity by private individuals, when taken out of the nest at a young age by unfavourable weather conditions.

Domestic chickens, *Gallus gallus domesticus*, were housed at a stable yard in Piddinghoe, Newhaven in East Sussex and tested from June to August 2019. Flock consisted of thirteen female individuals and one rooster, hatched in 2017 or 2018. The chickens had outdoor and indoor access during the day and were kept in a shed at night. Ten female domestic chickens were selected based on their tameness and willingness to follow the experimenter into a spacious test enclosure, visually and spatially separated from all other individuals. One individual was excluded from the experiment due to becoming agitated and reluctant to enter the test area in the course of the experiment. Chickens were rewarded with grapes.

All procedures were conducted in accordance with the ASAB/ABS guidelines for the treatment of animals in behavioural research. Experiments complied with Austrian and UK government guidelines. As experiments were entirely non-invasive, no further animal experimental license was required. Experiments on domestic chickens have been approved by the School of Life Sciences ethics panel at Anglia Ruskin University. All individuals participated and entered the experimental compartments voluntarily. Individuals were held in captivity before and after completion of the present study.

Experiment 1: The Detour Task

Four crows, two males and two females, and nine chickens were tested in this task. Due to time constraints, not all individuals could be tested. The experimenter placed a food reward in an opaque cylinder (approximately 30 cm in length and 10 cm in diameter), while the focal individual was watching. The cylinder needed to be sufficiently long so that the birds could obtain the reward at the centre of the cylinder by inserting their head through the opening, but not too large so that the birds could not enter the cylinder with their whole body. Crows received ten trials per session,

chickens received five trials per session, in order to keep motivation of individuals high. A correct response was considered when an individual retrieved the reward from either of the openings, without any prior contact with the long side of the cylinder. In order to pass the first stage of the detour task, individuals were required to complete at least five successful retrieves in a row. Once the first stage of the experiment was completed, individuals were presented with the transparent cylinder. Similar to the first stage, a food reward was placed in the cylinder in front of the focal individual. Crows received one test session consisting of ten trials and chickens two test sessions consisting of five trials. Therefore, overall, each individual received ten trials. The number of correct responses, *i.e.* individuals reaching directly to the reward without touching the long side of the cylinder first, was recorded similarly to stage one of the experiments.

Experiment 2: The Reversal Task

Eight crows, three males and five females, and nine chickens participated in this experiment. Data on learning performance from four focal crows has been previously published (Teschke et al., 2013). The apparatus consisted of two feeders that were mounted 30 cm apart on a wooden board. Feeders could be covered with paper lids of different colours (orange and blue). Prior to the test, a habituation period was conducted, familiarizing the focal individuals with the test apparatus and procedure. First, individuals were habituated to take rewards from the feeders, afterwards, feeders were partially covered with a white lid, training individuals to comfortably remove the lid in order to retrieve the reward. In each trial a reward was placed in one of the feeders behind a barrier and out of view of the focal animal. The lids were placed on the feeders and the apparatus positioned in front of the focal individual, who was then allowed to remove one of the two lids. The experiment consisted of two phases: an initial acquisition phase and a reversal phase. In the acquisition phase, one colour was the rewarded (S+) stimulus, half of the birds started with orange as S+ the other half

with blue as S+. The success criterion for the acquisition phase was that 80 % of ten trials were correct over two consecutive sessions or 100 % of ten trials correct in one session. Once a subject met criterion the colour-reward contingency was reversed in the reversal phase. In the acquisition phase, subjects were given a maximum of 140 trials to reach learning criterion, which one domestic chicken did not reach and consecutively was not tested in the reversal phase of the experiment. Tests of two further chickens and one crow could not be completed in the reversal phase due to time constraints. When a subject developed a positional bias (side bias), that is, when it chose one side in six consecutive trials, a side bias correction procedure was applied until that subject chose the non-preferred side once, whereupon we reverted to the normal pseudo-randomized trial schedule. Test sessions consisted of ten trials each. The rewarded side was pseudo-randomized, with each side being rewarded five times per session for the crows and maximum number of rewarded trials on one side was seven and minimum of times a side was rewarded in one session was three in the chickens.

Statistical analysis

Statistical analysis was performed in R v. 3.5.3 (The R Foundation for Statistical Computing, Vienna, Austria, http://www.r-project.org). Exact Wilcoxon-Mann-Whitney tests were computed. Spearman rank correlations were calculated using the package Hmisc (Harrell & Dupont, 2019). All datasets and the R script used to conduct the statistical analyses are available as supplementary files.

Results

Individual performance in the cylinder task ranged from 30 to 100 % correct trials in crows (mean ± SD: 73 ± 31) and 10 to 40 % correct trials in domestic chickens (mean ± SD: 23 ± 12). Crows performed better in the cylinder task compared to domestic chickens (Wilcoxon-Mann-Whitney Test: $W = 3$, $n_{chickens} = 9$, $n_{crows} = 4$, $p = 0.023$; Figure 1).

In the acquisition phase of the experiment, individual performance in crows ranged from 31 to 118 trials until learning criterion was reached (mean ± SD: 73 ± 33) and in domestic chickens from 30 to 140 trials (mean ± SD: 71 ± 39). In the reversal phase, crows' performance ranged from 56 to 200 trials until learning criterion was reached (mean ± SD: 122 ± 51) and domestic chickens' performance ranged from 30 to 100 trials (mean ± SD: 87 ± 24), however it should be noted that three chickens did not complete the reversal phase of the experiment (Table 1). In the reversal learning experiment, species did not differ in the number of trials until learning criterion was reached (Wilcoxon-Mann-Whitney Test: acquisition phase: $W = 34.5$, $n_{chickens} = 9$, $n_{crows} = 8$, $p = 0.923$; reversal phase: $W = 12$, $n_{chickens} = 6$, $n_{crows} = 7$, $p = 0.221$).

In crows, individuals who needed fewer trials to reach learning criterion in the acquisition phase also needed fewer trials to reach criterion in the reversal phase (Spearman correlation: $r = 0.86$, $n = 7$, $p = 0.013$; Figure 2). This relationship was lacking in domestic chickens (Spearman correlation: $r = -0.14$, $n = 6$, $p = 0.796$; Figure 2). Performance in the learning task did not correlate with performance in the cylinder task in domestic chickens (Spearman correlation: acquisition phase: $r = 0.08$, $n = 9$, $p = 0.833$; reversal phase: $r = 0.48$, $n = 6$, $p = 0.329$; Figure 3a). As we have only tested four crows in the cylinder task, we could not calculate a correlation between learning

performance and performance in the cylinder task, but we graphically illustrated results in figure 3b.

Discussion

In the present study we describe the performance of crows and domestic chickens in a motor-inhibition task and a reversal learning task. In both tasks, we describe pronounced individual variation in performance in both species. In the reversal learning task, crows reached learning criterion after 30 to 130 trials in the acquisition phase of the experiment and 60 to 200 trials in the reversal phase. Domestic chickens reached learning criterion after 30 to 140 trials in the acquisition phase and 30 to 100 trials in the reversal phase of the experiment. Individual variation in cognitive performance only recently came into focus of comparative cognition research (Boogert et al., 2018). Presently, we can only speculate about the causes of individual differences in our sample. Individual differences in learning performance can be caused by physical characteristics of the environment (Pike et al., 2018), social factors (Dalesman, 2018) or differences in personality (Dougherty & Guillette, 2018). We also would like to highlight that voluntary participation in our experiments might have caused a selection bias, with 'braver' individuals participating, whereas 'shyer' individuals, especially in the chicken might not have been tested (Morton et al., 2013). Although our sample might have been biased we would like to highlight that we describe significant pronounced individual difference withing each species of our sample. Traditionally, cognition research often focusses on comparisons between a small group of species considered as 'cognitively complex' (Miller et al., 2019). Our results illustrate that certain cognitive abilities, *e.g.* learning abilities, might not differ between species considered as cognitively complex, *i.e.* crows, compared to species not considered to possess cognitively advanced skills, *i.e.* domestic chicken, however pronounced individual difference might exist within species.

One critical limitation of our study is the small sample size. We only tested four crows in the cylinder task, which makes statistical comparisons between but also within the tested species

difficult. Small sample sizes are not uncommon in comparative cognition. In the field of physical cognition, all studies conducted on corvids had a sample size smaller than ten (Farrar et al., 2020). This can be explained by various factors, for example, the limited availability of captive individuals for testing, the high training effort and connected to this large time investment to conduct cognitive tests. Opportunities to overcome these limitations could be multi-lab collaborative studies (Many Primates et al., 2019; Primates et al., 2019) or meta-analyses (*e.g.*, (Dougherty & Guillette, 2018)). The present study, despite the small sample size will contribute to the growing body of literature about learning abilities in different species and hopefully as such in future can be incorporated into larger-scale comparisons.

Our results suggest corvids to perform well and chickens to perform poorly in the cylinder task, which is in line with previous findings (Ferreira et al., 2020; Kabadayi et al., 2016). This could indicate better motor-inhibition in crows compared to chicken. Motor inhibition and other aspects of self-control, along with working memory and cognitive flexibility, is considered an integral part of executive functioning in humans (Diamond, 2013). It could be argued that higher motor inhibitory control in corvids compared to chickens allows them to selectively attend and supress prepotent motor impulses and therefore perform better in tasks requiring complex decision making processes, such as delay of gratification (Dufour et al., 2012; Hillemann et al., 2014), inequity aversion (Wascher & Bugnyar, 2013), tactical deception (Bugnyar, 2013), mental time travel (Clayton & Dickinson, 1998), and causal reasoning (Schloegl et al., 2009). However, it also needs to be noted that chickens in previous tasks could learn to solve a detour task (Scholes, 1965) and that poor performance can be explained by perceptual and motivational factors (Regolin et al., 1994).

In the reversal learning task, crows and domestic chickens did not differ in performance, measured in the number of trials until learning criterion was reached, neither in the acquisition phase, nor the reversal phase of the experiment, although it should be noted that three chickens and one crow did not reach learning criterion. These results are in contrast to a previous study, red-billed blue magpies, *Urocissa erythroryncha*, outperformed white leghorn chicken in a serial reversal task (Gossette et al., 1966), but they highlight the importance of replicating results of previous studies and not drawing final conclusions about cognitive abilities of species from a limited sample of individuals.

Next to individual variation in cognitive performance, another aspect of comparative cognition which needs to be taken into consideration is the question which cognitive abilities different tests actually assess. One main advantage of the cylinder task is that it is easy and quick to conduct. The task requires low levels of habituation and training and can be successfully applied in a wide variety of species and thus has been widely applied to assess motor inhibitory control (Kabadayi et al., 2018; MacLean et al., 2014). However, the task is not uncontroversial and several authors question its suitability to assess motor inhibition (Farrar et al. 2020; van Horik et al., 2018, 2020), especially supported by the fact that task performance is poorly correlated with other measures of inhibitory control (Bray et al., 2014; Brucks et al., 2017; Vernouillet et al., 2018). In dogs, inhibitory performance was not correlated across different tasks (Bray et al., 2014; Brucks et al., 2017). We can exclude that domestic chickens had prior experience with transparent materials, however crows might have had prior experience, for example with transparent plastic bottles, provided as enrichment to the captive crows. Several studies evidence a lack of correlation in performance between the acquisition and reversal learning phase (Guido et al., 2017).

In conclusion, in our experiments crows seem to possess better motor-inhibitory control compared to domestic chickens. In contrast, learning performance in a reversal learning task did not differ between crows and domestic chickens. The sample size of our study is too small to draw final conclusions about differences or similarities in cognitive performance between the species, however we found notable individual differences in performance in both species.

Acknowledgements

We thank Christian Schloegl for assistance with the experimental procedure while conducting the cylinder task.

Conflict of interest

The authors declare no conflict of interest

Author contributions

Conceptualization: CAFW and GS; Data collection: CAFW, KA and GS; Formal analysis: CAFW; Writing: CAFW, KA and GS.

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Table 1. Individuals tested in the present study. Number of trials until learning criterion is reached in the acquisition and reversal phase of the learning experiment as well as percentage of trials correct in the cylinder task. Missing values indicates that the respective individual has not completed the task (reversal task: three chickens; cylinder task four crows).

Name	Species	Sex	Acquisition	Reversal	Cylinder Task
Baerchen	crow	male	31	62	100
Gabi	crow	female	50	90	
Peter	crow	female	65	107	90
Toeffel	crow	female	118	160	
Klaus	crow	male	33	56	70
Resa	crow	female	102		30
Nino	crow	female	90	200	
Walter	crow	male	95	159	
BG	chicken	female	100		10
DG	chicken	female	40	80	30
LB	chicken	female	30	90	20
N	chicken	female	60	30	20
O	chicken	female	140		40
P	chicken	female	60	90	40
WH	chicken	female	120		10
W	chicken	female	40	80	10
Y	chicken	female	50	100	30

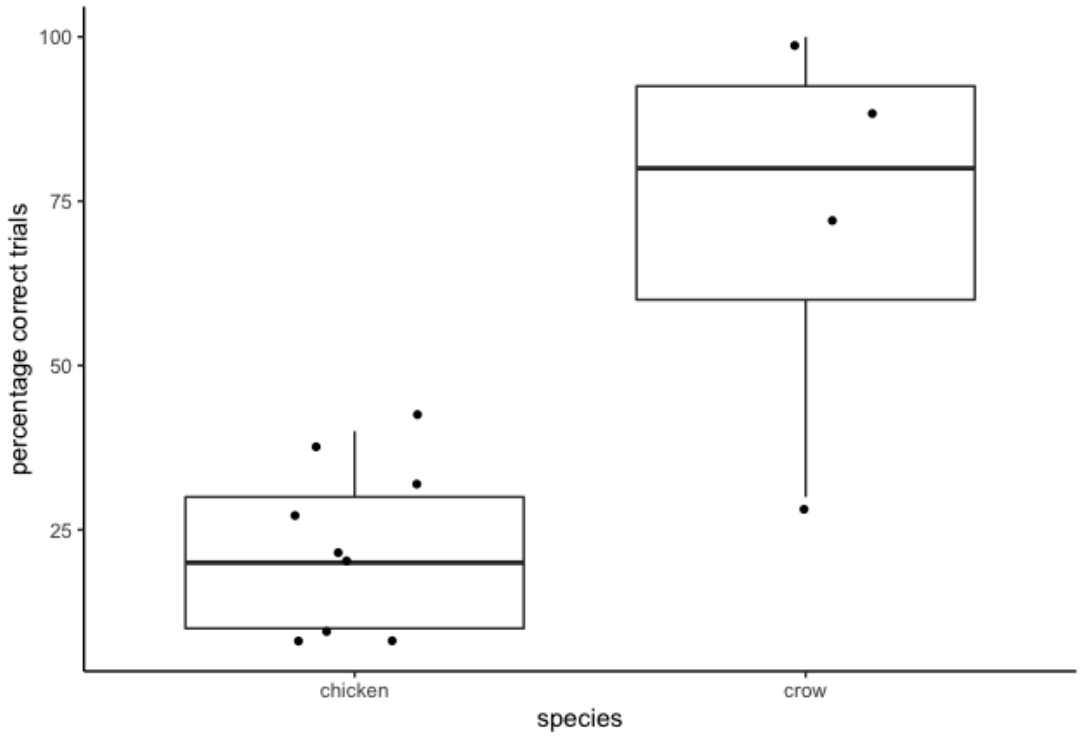

Figure 1. Percentage of correct test trials in the cylinder task. Box plots show the median and the interquartile range from the 25th to the 75th percentiles, black circles represent individual performance.

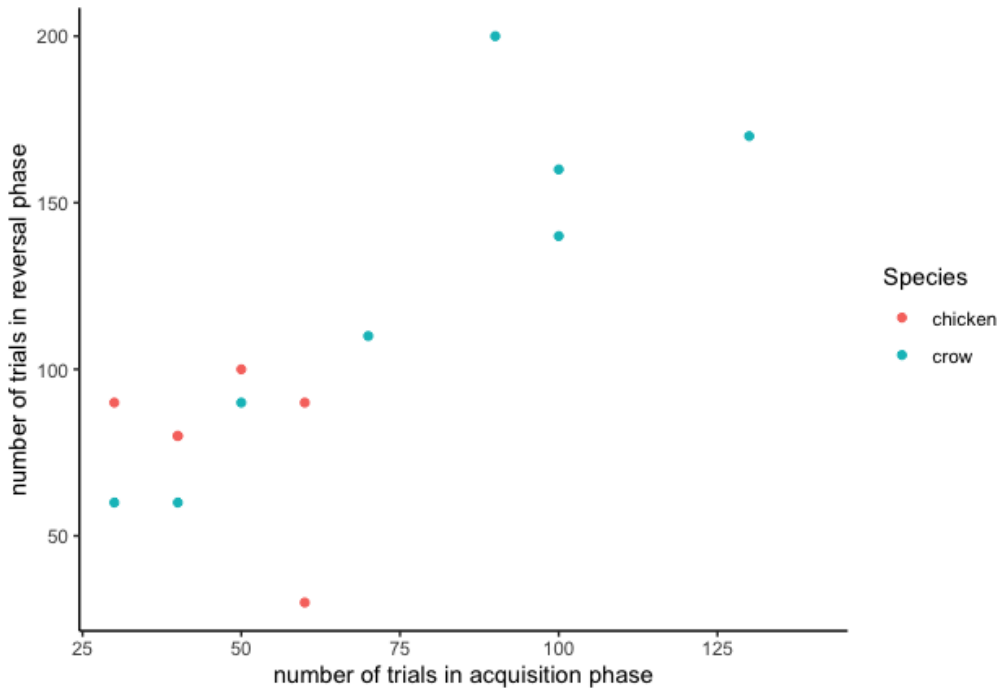

Figure 2. Relationship between learning performance in the acquisition phase (x-axis) and the reversal phase (y-axis) in crows (blue circles) and domestic chickens (red circles).

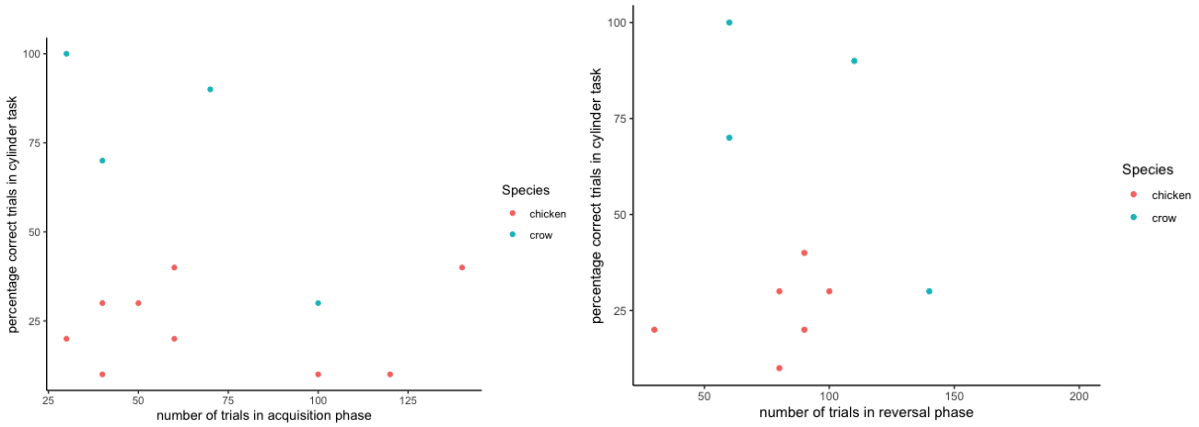

Figure 3. Relationship between learning performance in the acquisition phase (a) and reversal phase (b) on the x-axis and performance in the cylinder task (y-axis) in crows (blue circles) and domestic chickens (red circles).