Learning and motor-impulse control in domestic fowl and crows

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Abstract

Cognitive abilities allow animals to navigate through complex, fluctuating environments. For example, behavioural flexibility, which is the ability of an animal to alter their behaviour in response to a novel stimulus or to modify responses to as familiar stimulus or 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 compared performance of a captive group of eight crows, *Corvus corone,* and ten domestic fowl, *Gallus gallus domesticus*, 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. Four crows and nine fowl completed the cylinder task, eight crows completed the reversal learning experiment and nine fowl were tested in the acquisition phase, however three fowl did not complete the reversal phase of the experiment due to time constraints. Crows performed significantly better in the cylinder task compared to domestic fowl. 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 less trials to reach learning criterion in the acquisition phase also needed less trials to reach the criterion in the reversal phase. This relationship was lacking in domestic fowl. Performance in the learning task did not correlate with performance in the cylinder task in domestic fowl. Our results show crows to possess significantly better motor-inhibitory control compared to domestic fowl, which could be indicative of this specific aspect of executive functioning to be lacking in domestic fowl. In contrast learning performance in a reversal learning task did not differ between crows and domestic fowl, indicating similar levels of behavioural flexibility in both species.

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

Introduction

Cognitive abilities allow animals to navigate through complex, fluctuating environments. For example, an animals' ability to alter their behaviour in response to a novel stimulus and to modify responses to familiar stimuli is termed behavioural flexibility, which critically affects survival and fitness of individuals (Shettleworth, 2009). Similarly, changing environmental context might require the inhibition of previously successful behavioural strategies. 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 flexibility is the reversal learning task, where an individual has to learn a discrimination task and subsequently must respond to the previously unrewarded stimulus (Izquierdo et al., 2017). 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 comfortable to do 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 and detour to take the reward from the open ends is assessed (Kabadayi et al., 2018).

Cognitive flexibility and inhibitory control are expected to vary between and within species based on socio-ecological factors. 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). Next 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, 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 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 and carrion crows showed similar performance (Teschke et al., 2013). Corvids paralleled performance of great apes in a motor-inhibition task (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 fowl, *Gallus gallus domesticus.* Inhibitory control in fowl is related to keeping conditions. In a study by Ferreira et al. (2020) domestic fowl showed low levels of motor impulse control in the cylinder task. Impulse control was further affected by range, and high rangers showed a poorer performance compared to low rangers. 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 fowl 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 fowl 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. We expected to replicate previous findings of high levels of motor inhibition in crows, but not in chickens. Further, we expect corvids to learn a colour discrimination task quicker compared to chickens and to show higher behavioural flexibility.

Methods

Subjects and housing

Eight crows have been tested, 7 carrion crows, *Corvus corone corone,* and 1 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), either in male-female pairs or trios. 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 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 people, when taken out of the nest at a young age by unfavorable weather conditions.

Domestic fowl, *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. The fowl had outdoor and indoor access during the day and were kept in a shed at night. Ten female domestic fowl were selected based on their tameness and willingness to follow the experimenter into a spacious test enclosure. One individual was excluded from the experiment due to becoming agitated and reluctant to enter the test area in the course of the experiment. At the time of the experiments, fowl were approximately one to two years old. Fowl were rewarded with grapes.

Experiments complied with Austrian and UK government guidelines. As experiments were entirely non-invasive, no further animal experimental license was required. Experiments on domestic fowl 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 and nine fowl were tested in this task. The experimenter placed a food reward in an opaque cylinder, while the focal individuals were 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, this number had to be reduced to five trials per session for the domestic fowl, 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 fowl two test sessions consisting of five trials. Therefore, overall each individual received ten trials. The number of correct responses was recorded similarly to stage one of the experiments.

Experiment 2: The Reversal Task

Eight crows and nine fowl 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 colors (orange and blue). Prior to the test, a habituation period has been conducted, stepwise familiarizing the focal individuals with the test apparatus and procedure. First, individuals were habituated to take rewards from the feeders, afterwards, feeders have been 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 outside the 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 color 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 trials were correct over two consecutive sessions. Once a subject met criterion the color-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 fowl did not reach and consecutively was not tested in the reversal phase of the experiment. Tests of two further fowl 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 size was pseudo-randomized, with each side being rewarded five times per session in the crows and maximum amount 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 in the package coin (Hothorn et al., 2006). 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 at https://osf.io/q4jyk/.

Results

Crows performed significantly better in the cylinder task compared to domestic fowl (Wilcoxon-Mann-Whitney Test: Z = -2.347, n_1 = 9, n_2 = 4, p = 0.02; Figure 1). Individual performance in the cylinder task ranged from 30 to 100 percent correct trials in crows and 10 to 40 percent correct trials in domestic fowl. In the reversal learning experiment, species did not significantly differ in the number of trials until learning criterion was reached (Wilcoxon-Mann-Whitney Test: acquisition phase: Z = -0.29, n_1 = 9, n_2 = 8, p = 0.792; reversal phase: Z = -1.559, n_1 = 6, n_2 = 8, p = 0.129). In the acquisition phase of the experiment, individual performance in crows ranged from 30 to 130 trials until learning criterion was reached and in domestic fowl from 30 to 140 trials. In the reversal phase, crows' performance ranged from 60 to 200 trials until learning criterion was reached and domestic fowls' performance ranged from 30 to 100 trials, however it should be noted that three fowl did not complete the reversal phase of the experiment (Table 1).

In crows, individuals who needed less trials to reach learning criterion in the acquisition phase also needed less trials to reach criterion in the reversal phase (Spearman correlation: r^2 = 0.84, n = 8, p = 0.008; Figure 2). This relationship was lacking in domestic fowl (Spearman correlation: r^2 = 0.48, n = 6, p = 0.329; Figure 2). Performance in the learning task did not correlate with performance in the cylinder task in domestic fowl (Spearman correlation: acquisition phase: r^2 = 0.08, n = 9, p = 0.833; reversal phase: r^2 = 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 crows to perform significantly better in a motor-inhibition task compared to domestic fowl. This is in line with previous results, suggesting corvids to perform well and fowl to perform poorly in the cylinder task (Ferreira et al., 2020; Kabadayi et al., 2016). This could indicate better motor-inhibition in crows compared to fowl. 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 fowls 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).

In the reversal learning task, crows and domestic fowl 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 individuals have not been tested until learning criterion was reached, due to time constraints. This is surprising as we would generally have expected a higher cognitive performance in crows compared to domestic fowl. In a previous study, red-billed blue magpies, *Urocissa erythroryncha*, significantly outperformed white leghorn chickens in a serial reversal task (Gossette et al., 1966). Our results highlight the importance to test a wide variety of species in order to draw final conclusions about the convergent evolution of cognitive skills in distantly related taxa. Traditionally, cognition research often focusses on a small group of species considered as ‘cognitively complex’ (Miller et al., 2019), but we suggest that more studies on ‘control species’ lacking cognitive abilities in question are needed. 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 fowl.

Further, in the reversal learning experiment we show pronounced individual differences in performance in both species tested. 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 fowl 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 physical characteristics of the environment (Pike et al., 2018), social factors (Dalesman, 2018) or differences in personality (Dougherty & Guillette, 2018).

In our experiment, we only found limited evidence for repeatability of cognitive performance. In crows, learning performance between the acquisition and reversal phase of the learning experiment was positively correlated. This relationship was lacking in domestic fowl. Further, we did not find a relationship between performance in the reversal learning experiment and cylinder task, neither in crows nor in domestic fowl. A lack of replicability of test results is a general issue in comparative cognition research (Farrar et al., 2020). In our case, the lack of replicability of individual cognitive performance between the learning experiment and cylinder task certainly can be due to small sample size and low power. However, the lack of correlation between performance in different tasks is certainly not a unique phenomenon in comparative cognition.

In dogs, inhibitory performance was not correlated across different tasks (Bray et al., 2014; Brucks et al., 2017). Wolves performed significantly poorer in the cylinder task compared to dogs, suggesting that domestication could affect inhibitory control (Marshall-Pescini et al., 2015). Several studies evidence a lack of correlation in performance between the acquisition and reversal learning phase (Guido et al., 2017).

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. However, the task is not uncontroversial and several authors question its suitability to assess motor inhibition (Farrar et al. 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). Size and material of the tube might matter. Cats performed best on larger cylinders (Bobrowicz & Osvath, 2018). Further, impulse control assessed in the cylinder task has been shown to be significantly affected by prior experience with transparent materials (van Horik et al., 2018) as well as response learning (van Horik et al., 2020). We can exclude that domestic fowl 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.

In conclusion, the results of our experiments show crows to possess significantly better motor-inhibitory control compared to domestic fowl, which could be indicative of this specific aspect of executive functioning to be lacking in domestic fowl. In contrast learning performance in a reversal learning task did not differ between crows and domestic fowl, indicating similar levels of behavioural flexibility in both species.

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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 fowl; cylinder task four crows).

Name	**Species**	**Sex**	**Acquisition**	**Reversal**	**Cylinder Task**
Baerchen	crow	male	30	60	100
Gabi	crow	female	50	90	
Peter	crow	female	70	110	90
Toeffel	crow	female	130	170	
Klaus	crow	male	40	60	70
Resa	crow	female	100	140	30
Nino	crow	female	90	200	
Walter	crow	male	100	160	
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

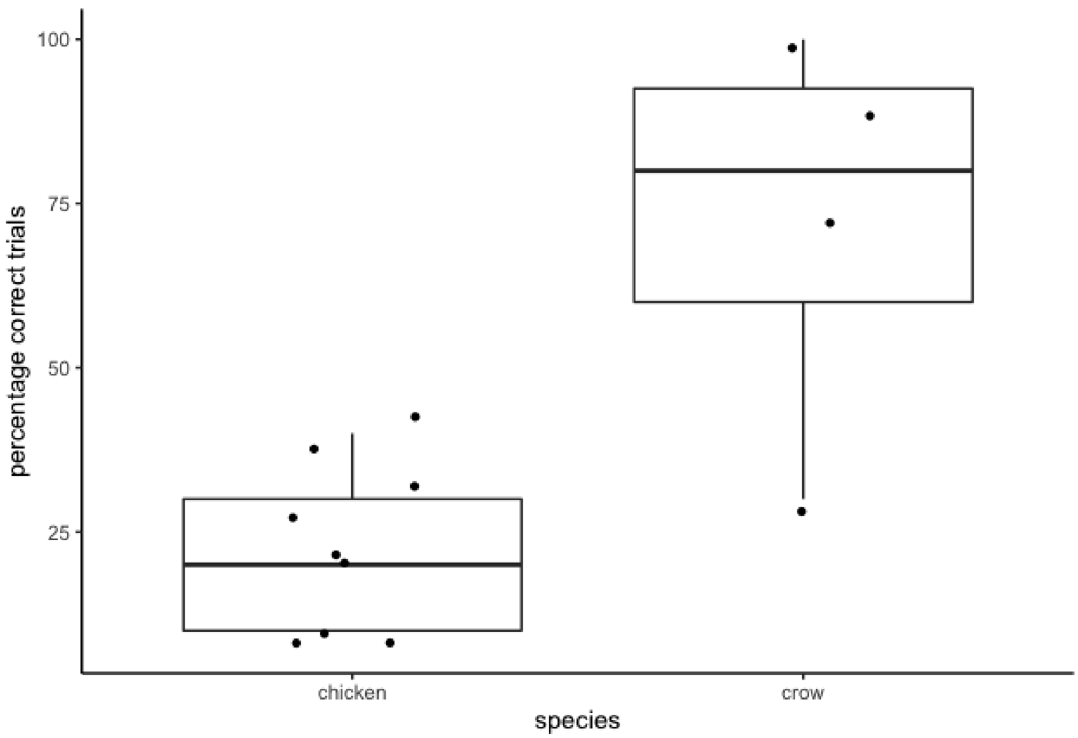

Figure 1. Percentage of correct test trials in the cylinder task. Box plots show the median and the interquartile range from the 25th to the 75th percentiles, black circles represent individual performance.

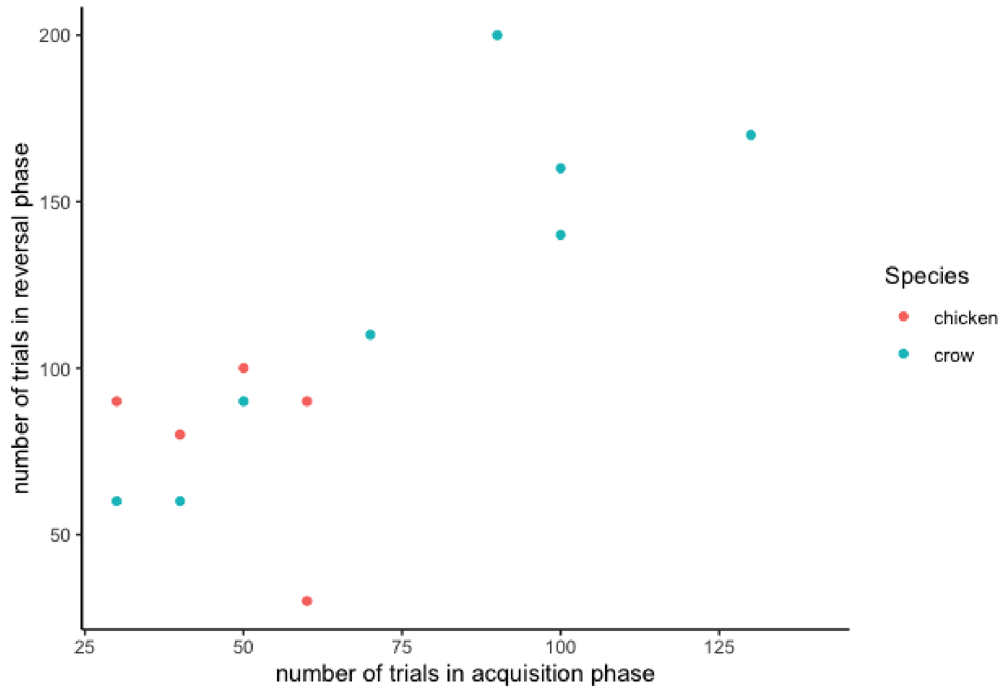

Figure 2. Relationship between learning performance in the acquisition phase (x-axis) and the reversal phase (y-axis) in crows (blue circles) and domestic chickens (red circles).

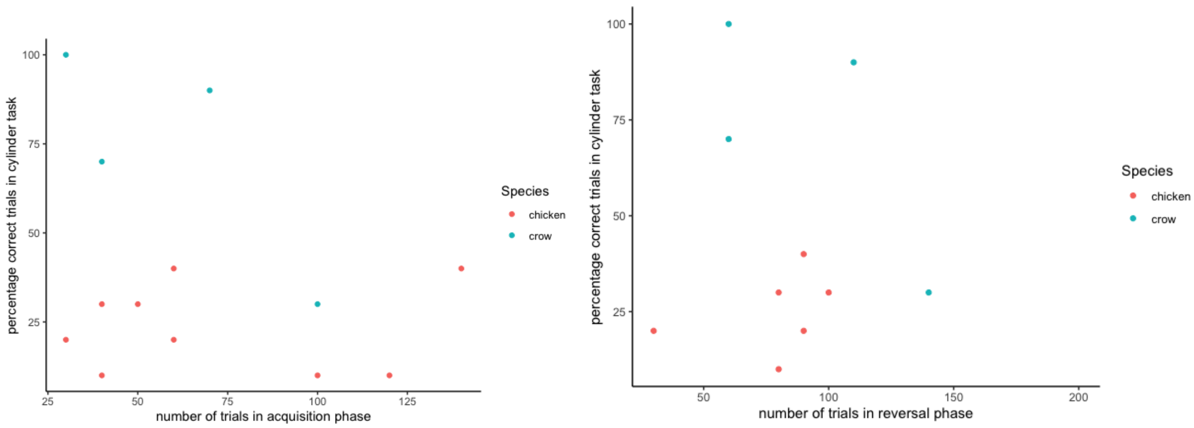

Figure 3. Relationship between learning performance in the acquisition phase (a) and reversal phase (b) on the x-axis and performance in the cylinder task (y-axis) in crows (blue circles) and domestic chickens (red circles).