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Animal behaviour

Uninhibited chickens: ranging behaviour impacts motor self-regulation in free-range broiler chickens (*Gallus gallus domesticus*)

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Inhibiting impulsive, less flexible behaviours is of utmost importance for individual adaptation in an ever-changing environment. However, problem-solving tasks may be greatly impacted by individual differences in behaviour, since animals with distinct behavioural types perceive and interact with their environment differently, resulting in variable responses to the same stimuli. Here, we tested whether and how differences in ranging behaviour of free-range chickens affect motor self-regulation performance during a cylinder task. For this task, subjects must refrain from trying to reach a food reward through the walls of a transparent cylinder and detour to its open sides, as a sign of inhibition. Free-range chickens exhibited an overall low performance in the motor self-regulation task ($31.33 \pm 13.55\%$ of correct responses), however, high rangers showed significantly poorer performance than the low rangers ($23.75 \pm 9.16\%$ versus $40 \pm 12.90\%$, respectively). These results give further support to the impacts of individual behavioural differences on cognitive performances. This is the first demonstration to our knowledge of a relationship between exploratory tendencies and motor self-regulation for an avian species.

1. Introduction

Inhibiting impulsive, less flexible behaviours is of utmost importance for individual adaptation in ever-changing environments. The faster an individual copes with new situations, suppressing counterproductive, prepotent responses and switches to more appropriate reactions, the better its chances of surviving and reproducing [1–4].

In humans, behavioural inhibition occurs actively not only when a movement needs to be stopped, but also in the anticipation of a stop event or during an action preparation [5]. For non-human animals, a familiar method to assess behavioural inhibition is the cylinder task (also known as detour-reaching task). For this task, subjects must refrain from trying to reach a food reward through the walls of a transparent cylinder and detour to its open sides, as a sign of inhibition [6]. Previous studies have shown that this task reveals motor self-regulation in mammals, birds and fish [7–9]. However, a recent study showed that some individuals were more consistent in inhibiting their behaviour than others, suggesting large inter-individual variability and a need for consideration of individual reaction patterns when studying behavioural inhibition in animals [10].

Figure 1. (a) Transparent cylinder used during habituation and (b) cylinder used during training (opaque) and test phases (transparent). Letters indicate the position of superworms across the three phases of training. The last phase of training as per the tests, only one superworm was in the centre of the cylinder.

The direction of the relationship between cognitive performances and individual behavioural differences is still poorly understood [11]. Animals from the same population or group submitted to the same conditions may still perceive and interact with their environment differently, which results in varying responses to the same stimuli [12,13]. Exploratory behaviour, for example, is considered to be an important modulator of cognitive performances in diverse tasks [14,15]. Therefore, variation in exploratory behaviour is also expected to modulate how animals inhibit and regulate their motor responses. To date, research testing avian species for both exploration and motor self-regulation has not established any significant parallel between these two components [16,17].

In this study, we tested whether and how differences in the ranging behaviour of free-range chickens affect motor self-regulation performance during a cylinder task. The recent literature on free-range chickens and junglefowl has confirmed the influences of animal personality on cognition [18,19]. We recently showed that differences in ranging behaviour in free-range chickens were stable across time (indicative of a personality trait) and influenced spatial memory performances, with less exploratory chickens showing better spatial memory when compared to high exploratory ones [20]. For junglefowl, less exploratory hens were faster at reversal learning and more fearful junglefowl chicks exhibited higher flexibility [14,18]. We therefore hypothesized that differences in ranging behaviour would have an impact on behavioural inhibition, with high levels of ranging behaviour being indicative of little flexibility and resulting in poorer motor self-regulation when compared to birds with low levels of ranging behaviour.

2. Material and methods

Nineteen free-range male broiler chickens (*Gallus gallus domesticus*) were selected for the motor self-regulation task, based on their ranging level (after range observations, individual chickens ranging closer to the poultry house were considered low rangers and those who ranged further were considered high rangers). The chickens had no previous contact with transparency, nor with any type of behavioural or cognitive testing. See electronic supplementary material for information on animal housing and husbandry, ranging behaviour measurement and individual selection [21].

(a) Motor self-regulation task

The task was conducted on 19 selected chickens, from 77 to 102 days of age. Chickens were separated into two groups of 10 and 9 individuals, tested every other day. In the morning, a group of chickens was captured, taken to the test room and placed in an enclosure with a straw-covered floor and ad libitum water, but no food. Chickens waited for at least 4 h before the beginning of the tests in order to standardize food motivation among individuals. The individual order of testing was kept similar throughout the experiment. See electronic supplementary material for further details on task procedures.

(i) Habituation

For 3 days chickens were gradually habituated to being alone in the test arena (square enclosure with opaque walls and a vinyl floor, $1 \times w \times h$: $1 \text{ m} \times 1 \text{ m} \times 2 \text{ m}$) and to its components (cylinders, transparency and superworms, *Zophobas morio*). During the third and last day of habituation, each chicken was allowed 10 min free access to the arena containing a small transparent cylinder (different from the one used during testing, figure 1a) surrounded by five superworms. For this particular day, we recorded the latency to eat all five superworms (in seconds) as a proxy measure for food motivation. By the end of habituation, all birds consumed the superworms in less than 2 min.

(ii) Training

Training occurred in the same arena and consisted of three phases during which the number of superworms was gradually decreased (five, three and one superworms, successively) near or inside an opaque cylinder fixed horizontally on a wooden platform ($l \times d \times h$: $20 \times 10 \times 26 \text{ cm}$, figure 1b). The goal was to teach individuals to detour either side of the cylinder and eat the superworm at its centre. Each chicken was given a maximum of eight consecutive trials per day. In each trial, the individual had a maximum of 1 min to eat all the superworms. The trial was considered a success if the individual ate all of the superworms within 1 min. For individuals that failed to find the reward or did not move, the experimenter gently approached and guided (by gently touching or blocking movement away from the cylinder) the bird towards one of the cylinder's open sides to facilitate access to the superworms for an additional minute. Individuals with four consecutive successful trials moved on to the next phase. Once a chicken successfully passed the three phases, the individual was able to undergo inhibition tests. Variables considered within the training phase were: the total number of trials and total latency (in seconds) spent on training.

(iii) Test

For the test, the opaque cylinder was replaced by a transparent cylinder with the same dimensions. Procedures were similar to the last phase of training (one superworm at the centre of the cylinder). Individuals were submitted to test trials (a maximum of eight trials per day) with the transparent cylinder until reaching 10 active trials (with a correct or incorrect response). Correct trials were coded when the individual detoured through the sides of the cylinder (without pecking at the walls), and reached and ate the superworm within 1 min. Incorrect trials were coded when the individual's first reaction was to try and reach the superworm by pecking through the walls of the cylinder. We recorded both correct/incorrect trials and latency to eat the superworm. Trials where individuals did not interact with the cylinder within the first minute (inactive trials) were not considered.

(iv) Statistics

To investigate the relationship between ranging level and food motivation during habituation (latency to eat all five superworms) and training performance (total number of trials and total latency to successfully pass all three training phases), we ran a Mann–Whitney test using ranging level (low and high ranger) as the group variable.

For the test, we analysed correct/incorrect trials with generalized linear mixed models (GLMM, 'lme4' R package) fitted for binary data. Latency to eat the superworm (log-transformed) was analysed using a linear mixed model (LMM, 'lmerTest' R package) and degrees of freedom were estimated through the Satterthwaite approximation. For both models, ranging level and test trial number (1–10) were added as fixed factors and individual ID was considered a random factor to account for repeated observations. The interaction between the ranging level and test trial number was not significant and was excluded from the final models. We also ran a Wilcoxon test to compare changes in performance between the first five and the last five test trials for both groups separately, followed by a Mann–Whitney test to compare the groups within these two periods.

Differences between high and low rangers on the number of inactive test trials (without interaction with the cylinder) were compared using a Mann–Whitney test. All non-parametric analyses were done using Monte Carlo simulation.

All statistical analyses were performed using IBM SPSS 21 and R v. 3.6.1. Statistical significance was accepted at $p \leq 0.05$. Results are presented as raw mean $\pm$ s.d. Four individuals (two low rangers and two high rangers) did not succeed during training and therefore 15 individuals (seven low rangers and eight high rangers) went on to the final test. Data from excluded individuals were not included in the statistical analyses.

3. Results

There was no significant difference between groups for the latency to eat five superworms during the last day of habituation (low rangers: 44.52 ± 24.5 ; high rangers 26.87 ± 12.92 ; $U = 17.5$, $p = 0.248$), nor for training performance (total number of trials and total latency to successfully pass all three training phases, low rangers: 33.85 ± 14.45 ; high rangers 29.37 ± 12.69 , $U = 22$, $p = 0.504$; low rangers: 1542 ± 1050.96 ; high rangers 1106 ± 624.25 , $U = 20$, $p = 0.406$, respectively).

The percentage of correct trials during the 10 trial tests for the free-range chickens was $31.33 \pm 13.55\%$. Performance on the task was influenced by both trial number ($\chi^2_1 = 9.726$, $p = 0.001$) and ranging level ($\chi^2_1 = 4.81$, $p = 0.028$). Correct

Figure 2. Percentage of correct test trials between the first five and last five trials ($n_{\text{low rangers}} = 7$, $n_{\text{high rangers}} = 8$). The lines indicate mean percentage of correct test trials for low rangers (upper line), all chickens combined (middle line) and high rangers (lower line), respectively. Data are presented as mean $\pm$ s.d.

test trials significantly increased with the trial number and low rangers ($40 \pm 12.90\%$) were significantly more successful than high rangers ($23.75 \pm 9.16\%$). Further analysis revealed that differences between groups occurred mainly during the last five trials. Low rangers tended to improve their performance between the first and the last five trials (from $22.85 \pm 21.38\%$ to $57.14 \pm 21.38\%$, $Z = -2.014$, $p = 0.063$), whereas high rangers did not show signs of improvement (from $20 \pm 15.11\%$ to $27.5 \pm 18.32\%$, $Z = -0.750$, $p = 0.630$). The percentage of correct trials did not differ between groups within the first five trials ($U = 27$, $p = 0.950$) but did so during the last five trials ($U = 8.5$, $p = 0.030$, figure 2).

The latency to eat the superworm decreased significantly across test trials ($\chi^2_1 = 15.273$, $p < 0.001$), without influences of ranging level ($\chi^2_1 = 1.497$, $p = 0.221$). Finally, the number of inactive test trials did not differ between groups (low rangers: 1.14 ± 0.89 , high rangers: 1.5 ± 2.5 , $U = 24.5$, $p = 0.677$).

4. Discussion

Free-range chickens exhibited an overall low performance in the motor self-regulation task, attaining similar results to other birds tested to date [7]. Beyond average performance, high rangers had the worst performance of all species tested thus far [7,8,10,22–26]; low rangers, however, attained higher levels of inhibition, comparable to those of some monkeys and prosimians [7]. Low rangers also tended to improve their performance between their first five and last five trials, outperforming high rangers during the last five trials.

Recent research on junglefowl and free-range laying hens/broiler chickens have been gradually accumulating evidence for the existence of proactive–reactive coping style strategies [27]. Chickens presenting low range use are more fearful, more vigilant, more passive and exhibit a higher corticosterone response during stressful situations than high rangers [28–31]. These reactive characteristics may, therefore, impact how the individual will cognitively perceive its environment: reactive individuals are expected to pay more attention to environmental changes and to be more flexible than proactive ones [32,33]. In junglefowl chicks, fearfulness,

behavioural flexibility and generalization of learned preferences are all positively linked [34]. Our findings provide support to the relationship between different behavioural types and different cognitive styles where some individuals favour immediate rewards, are more impulsive, and less accurate in their decision process, while others are more risk-averse about rewards, less impulsive and more accurate [33].

As evidenced by the significant effect of trial number on correct trials and latency to eat the superworm, some learning did occur during the tests [6,35]. Chickens performed better in the last five trials compared to the first five trials. Santos *et al.* [36] suggested that insufficient training trials may result in increased performance across test trials. However, caution needs to be taken with overtraining animals as they may establish strong stimulus–response habit solutions, resulting in misleading high performances [37,38]. As our low and high rangers performed similarly during habituation and training, and still groups had different performances during test trials, the most plausible explanation for learning during tests is that chickens' lack of experience with transparency in the first trials resulted in poor initial performance [23], and, as trials progressed, animals became more accurate and faster, as was the case for Clark's nutcrackers (*Nucifraga columbiana*) and pheasants (*Phasianus colchicus*) [38,39].

The environmental complexity of different housing conditions and internal factors such as sex, breed and

animal personality are known to affect an individual's behaviour, brain morphology and cognitive abilities [14,40–44]. In our study, animals living under the same conditions but with different propensities to range showed different levels of motor self-regulation. These results give further support to the implications of individual behavioural differences for cognitive performances. To our knowledge, this is the first demonstration of a relationship between exploratory tendencies and motor self-regulation for an avian species.

Ethics. The experiment was conducted under INRAE ethics committee approval (APAFIS # 17824-2018112611585147 v4), in agreement with French legislation.

Data accessibility. Data available from the Dryad Digital Repository: <https://dx.doi.org/10.5061/dryad.s7h44j137> [21].

Authors' contributions. V.H.B.F., K.G., L.C. and V.G. conceived the study. L.R. executed the project and collected data. V.H.B.F. and L.R. analysed and interpreted data. V.H.B.F. was the primary author and drafted the initial manuscript, for which L.R., K.G., L.C. and V.G. provided critical revision and improvements. All authors revised the final draft, approved the final version of the manuscript and agree to be held accountable for the content therein.

Competing interests. We declare we have no competing interests.

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