To Peck or Not To Peck: The influence of early-life social environment on response inhibition and impulsive aggression in Japanese quails

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1. Summary

Deficits in response inhibition (i.e., the ability to suppress inappropriate responses) may contribute to increased impulsive aggression (i.e., unplanned behaviors that harm others). Since early-life environment might influence the development of response inhibition, it could also indirectly affect impulsive aggression. However, this relationship has rarely been directly examined. Here, we investigated whether response inhibition is associated with impulsive aggression and whether this relationship explains the effects of early-life social environments on impulsive aggression in Japanese quails (*Coturnix japonica*). Quails (n = 120) were raised in two social conditions: Small groups of five birds or Large groups of 15 birds. Response inhibition was assessed using the Barrier and Cylinder tasks, while impulsive aggression was measured in two contexts - within a group of five familiar individuals and in a dyad with an unfamiliar individual. We found that some aspects of response inhibition were related to impulsive aggression. Furthermore, quails reared in small groups showed significantly poorer response inhibition than those reared in large groups. Yet, impulsive aggression did not significantly differ between the two conditions. These findings suggest that, while impulsive aggression is partly related to response inhibition, other factors mitigate the effects of early social environments on its expression.

Keywords: aggression, early-life social environment, inhibitory control, impulsive behaviour, personality, response inhibition

2. Introduction

Group living brings many benefits, such as reducing predation pressure and increasing foraging efficiency, but can also create conflicts between members due to increased competition (1). These agonistic interactions between individuals may result in *impulsive aggression* (i.e., the unplanned behavioural response of inflicting damage to self or others, (2)), that in turn may sometimes have negative fitness consequences for one or multiple individuals involved (e.g., reduced access to resources, injuries, or even death). While a lot of research has focused on aggression as a personality trait in animals (as reviewed by e.g., (3)), little is known about the cognitive mechanisms underlying aggression.

Some researchers suggest that impulsive aggression results from deficits in *response inhibition* (also referred to in the animal cognition field as *inhibitory control*; (4–6); but see (7)), the suppression of inappropriate pre-potent behavioural responses or actions (8–10). Indeed, inhibition deficits are correlated with increased aggression in rats (11), dogs (12), long-tailed macaques (13), and humans (14–16). Additionally, both increased levels of aggression and decreased levels of response inhibition have been correlated with lower levels of central serotonin (5-HT), a well-conserved neuromodulator of nervous systems in both invertebrates and vertebrates (9,11,17,18). However, most studies investigating the link between response inhibition and impulsive aggression are correlational. This has two important consequences. First, response inhibition deficits could cause or contribute to impulsive aggression, but it is also possible that a common underlying factor simply influences both (independently) (as suggested by (19)). Second, it has been proposed that environmental factors during early life contribute to response inhibition deficits and impulsive aggression later in life. Yet again, causal relationships have been hard to establish, and systematic research is lacking.

Early-life environmental conditions, both physical and social, can shape an individual's cognitive abilities and personality (e.g., (20–24)). For example, response inhibition is key to

maintain spatial and temporal cohesion between group members (25). Indeed, individuals within a group benefit from being surrounded by others and performing the same activity together, so they need to adjust their activity to that of other group members (e.g., (26,27)). Additionally, within a group, subordinate individuals might inhibit feeding or mating in the presence of dominant individuals to avoid potential aggressive interactions or confrontations (28). Given that social complexity is multi-faceted and highly variable, both within and between species (29), in the present study we focused on one key aspect of the social organization – social group size (30). An increase in group size means an increase in potential interactions with other group members, and therefore an increase in possibilities to learn how to interact with other individuals. Social group size has been shown to correlate with higher levels of response inhibition in Australian magpies (*Cracticus tibicen dorsalis*, (31)), in hyenas (*Crocuta crocuta*, (32)), and in primates (33), but not in guppies (*Poecilia reticulata*, (24,34)). Hence, we expected that a larger group size required individuals to develop better response inhibition due to greater social requirements.

Many studies have found aggression is usually suppressed in larger groups (e.g., calves – (35), chickens – (36,37), fish – (38), pigs – (39)). Based on the same reasoning described in the previous paragraph, with larger groups come a higher number of potential competitors for resources, and individuals might thus benefit to switch to a more socially tolerant strategy (e.g., (37,40), but see e.g., (41)). Yet, methodological differences between studies make it difficult to determine whether, and if so in what direction, early-life social environment shapes an individual's aggressive tendencies (42). Based on previous research and on the theoretical link between inhibition and aggression, and because we predicted that individuals raised in larger groups would have better response inhibition, we expected levels of impulsive aggression to decrease with increasing group size.

In this study, we investigated the link(s) between early-life social environment, response inhibition and aggression in Japanese quails (*Coturnix japonica*). Japanese quails are a precocial social bird species that is easy to raise in captivity, which enabled us to rear them without the presence of

101 adult quails. This controlled raising environment allowed us to manipulate their postnatal social
102 conditions, while controlling all other environmental parameters. Additionally, Japanese quails have
103 long been recognized as an ideal model for studying aggression, as hierarchies within their social
104 group are established and maintained through frequent aggressive interactions (e.g., (26,43,44)). As
105 a result, their typical behaviors, including aggressive behaviors towards conspecifics, have been
106 extensively documented (e.g., (44–46)). These combined factors were crucial in establishing causal
107 relationships between early-life social environment and an individual's response inhibition and
108 aggression.

109 We evaluated response inhibition in Japanese quails with two commonly used tasks to
110 evaluate an animal's response inhibition: the *Barrier task*, during which individuals must detour
111 around a vertical transparent barrier to reach a reward, and the *Cylinder task*, during which
112 individuals must reach through the openings of a transparent cylinder to obtain a reward. Both
113 tasks are purporting to measure the same aspect of response inhibition and have been referred to
114 as "detouring" tasks or "motoric self-regulation" tasks, as, in both tasks individuals must inhibit a
115 prepotent motor action (i.e., going towards the visible reward) and instead change it into a different
116 one (i.e., detouring around a physical barrier) (47) (but see (48)). Aggression was evaluated in two
117 different contexts: once in a group of familiar individuals (e.g., (44)), and once in presence of an
118 unfamiliar individual (e.g., (49)).

119 The main goal of the study was to experimentally determine the influence of early-life social
120 environment on response inhibition and impulsive aggression in Japanese quails. We focused on
121 three research questions: (A) do deficits in response inhibition cause impulsive aggression at an
122 individual-level, and (B) does social group size during early life shape an individual's response
123 inhibition and (C) impulsive aggression? Based on previous correlational research and on
124 theoretical models, we predicted that, if indeed higher impulsive aggression can be attributed to a
125 deficit in response inhibition, (A) response inhibition and impulsive aggression would be inversely

126 related at an individual-level, and that (B and C) individuals raised in larger groups would have a
127 higher level of response inhibition and be less aggressive than individuals raised in smaller groups.

128 **3. Material and methods**

129

130 *Subjects*

131

132 We used 120 Japanese quails (*n* = 60 females, *n* = 60 males) in this study. Birds were hatched
133 simultaneously over two days and kept together at the Opvangcentrum Vogels en Wilde Dieren,
134 Ostend, Belgium. Birds were housed in four identical heated lofts, each loft containing four $1m^2$ (1
135 m length x 1 m width x 2 m height) enclosures. Each enclosure included an electric hen heating
136 plate (25 cm length x 25 cm width, Comfort Chicks), which was replaced with a plastic cover when
137 birds were 16 days old. Outside of the experimental food restriction procedure, birds were provided
138 with *ad lib* grain food mix (Aveve), presented in a single 50-cm long linear chick feeder (Voss
139 Framing). Birds had free access to water. Each loft followed a 12:12 day-night cycle, with light
140 onset at 07:00 am. All birds were visually checked at least twice a day (once in the morning and
141 once in the evening). Measurements (weight and tarsus length) were taken when the birds were 20
142 days old (before the start of the study) and at 44 days old (at the end of the study). Quail care was
143 performed by AV, KW, RA, AD, WZ, and CT, under AV and RA's supervision.

144 Within each loft, one of the four enclosures housed a large group of 15 individuals (Large),
145 and the three other enclosures housed a small group of five individuals (Small). On day 2 post-
146 hatch, birds were randomly assigned to either a Small or a Large enclosure. Hence, 60 birds were
147 assigned to each experimental condition.

148

149 *General Experimental Procedures*

150

151 Quails were habituated to being handled and to the testing environment during their second
152 and third week. Testing started when birds were 24 days old. All 120 individuals underwent the
153 Barrier task, the Cylinder task, the Familiar Group task, and the Unfamiliar Individual task, given
154 in that order for all individuals. Birds were tested individually during the Detour and the Cylinder
155 tasks (i.e., response inhibition tasks), and with other individuals during the Familiar Group and the
156 Unfamiliar Individual tasks (i.e., impulsive aggression tasks), and tasks were performed on separate
157 days. A schematic overview of the study timeline can be found in the Supplementary Material (Fig.
158 S1).

159 Testing took place between 08:30 and 14:00 (local time). Food was removed the evening
160 prior testing to ensure motivation to participate in the experiment. On the morning of testing, birds
161 were individually placed in a portable cage with multiple compartments (Ducatillon) and
162 transported to a waiting room, where they were kept before and after testing until all individuals
163 had been tested.

164 All testing occurred in a test box (86 cm length x 146 cm width x 91 cm height). The testing
165 box was lit with LED lights to control for lighting. All trials were recorded using a camera
166 (BASCOM) mounted to the ceiling of the test box. A 'start box' (29 cm length x 45 cm width x 29
167 cm height) was attached to the front of the test box. The start box had two doors – one transparent
168 and one opaque – which slid vertically on rails between the two boxes, and a separate light. Inside
169 the start box was another square piece of wood that served as the back of the box attached to a
170 handle, which could slide forward and was used to gently push the birds into the test box when
171 required.

172 Every testing trial followed the same general procedure. First, the bird(s) to be tested was
173 (were) placed in the start box with both start box doors closed. Next, the opaque door was opened,
174 allowing the bird(s) to see within the test box but not enter the test box. After 15 seconds the
175 transparent door was opened, indicating the start of the trial. Birds that did not leave the start box
176 within 30 seconds were gently pushed into the test box. Once the bird(s) either reached the reward

177 location, or the time limit for the trial was reached, the test box lights were turned off, indicating
178 the end of the trial. The bird(s) was (were) given 15 seconds to return to the start box; if it(they)
179 did not, it was (they were) caught by the experimenter and placed back in the start box. Once all
180 birds completed all required trials for a session, they were returned to their home enclosures. Data
181 collection was performed by AV, KW, RA, AD, WZ, CT, and LL, under AV and KW's supervision.
182 Videos were coded using BORIS v.7.13 (Behavioral Observation Research Interactive
183 Software (50)). All the videos of the response inhibition tasks were coded by one experimenter
184 (KW), who was naïve to the conditions. All the videos of the impulsive aggression tasks were coded
185 by another coder (SK), who was naïve to the conditions and the experimental hypotheses. To assess
186 inter-observer reliability, 20 % of the videos of the response inhibition tasks were coded by one
187 coder (SK), who was naïve to the conditions and the experimental hypotheses, and 20 % of the
188 videos of the impulsive aggression tasks were coded by one experimenter (AV). Inter-rater
189 reliability was calculated using BORIS, and was high, with average Cohen's kappa coefficients of
190 0.840 and 0.805, for all response inhibition videos and all impulsive aggression videos respectively
191 (51).
192
193 *Habituation*
194
195 Birds were gradually habituated to the portable cage from 20-days-old onwards and to the
196 test box at 22-23 days old. For the habituation in the test box, a feeder was placed 50cm from the
197 test box entrance. The feeder used was filled with grains and was the same design as those used in
198 the birds' enclosures, but smaller (30cm length). A petri dish with two live mealworms was also
199 placed in front of the feeder. Both rewards were familiar to the birds and were used to encite them
200 to participate in testing. The total trial time was 5 minutes; each bird received one habituation trial.
201

Response inhibition tasks

Barrier task

Apparatus. The apparatus for the Barrier task consisted of a square wooden frame (40 cm length x 41.2 cm height) with two horizontal supports (20 cm width) (Fig. 1). The frame was placed 55 cm from the entrance of the test box, centrally such that there was 22 cm between it and the test box wall on each side. A reward feeder filled with grains was placed directly behind the barrier, and a petri dish containing two mealworms was placed directly behind the feeder. An opaque barrier was used during the training trials and a transparent barrier was used during the testing trials, so the reward food was visible to the birds through the barrier during the test session (Fig. 1). Both barriers had a strip of green tape on the left side and a strip of yellow tape on the right side (the same colours as the enclosure and reward feeders).

Procedures. This task included a training session and a testing session on two separate, consecutive days.

During the training session, the opaque barrier was attached to the frame. During the first trial, the bird was given two minutes to detour around the barrier to reach the food; from the second trial onwards, it had one minute and a half. Trials were repeated until the bird successfully detoured on three consecutive trials, with a maximum of seven trials per bird. If the bird did not detour once within three consecutive trials, the session ended. All birds passed the training session.

The testing session on the following day consisted of one training trial and one test trial per bird. The test trial followed the same procedure as during the training trials, but the transparent barrier was used instead of the opaque barrier.

'Successful' trials were defined as when the bird detoured around the barrier (opaque or transparent) without interacting (i.e., pecking or pushing) with it.

228

229 Cylinder task

230

231 *Apparatus*. The cylinder apparatus consisted of a transparent Plexiglas tube with open ends
232 (5.4 cm diameter x 13.2 cm length) mounted on a small wooden platform (13 cm length x 3 cm
233 width x 2 cm height; Fig. 1). The wooden base was covered with horizontal strips of yellow and
234 green tape. The apparatus was placed 40 cm from the entrance of the test box, so that the entrances
235 were perpendicular to the start box and secured to the floor with tape. One freshly killed mealworm
236 and 1tsp of grain were placed centrally inside the cylinder. Quails had to put their head within the
237 cylinder to retrieve the food.

238 *Procedures*. The Cylinder task occurred during a single test day. During each trial, the bird
239 had two minutes to reach the food inside the cylinder. Trials were repeated until the bird completed
240 ten trials, which was the maximum number of trials given, or until the bird failed to reach the food
241 for three consecutive trials.

242 'Successful' trials were defined as when the bird reached the food through one of the two
243 open sides of the cylinder without first pecking at the outside of the cylinder.
244 For the purpose of this study, we will only focus on the first trial, as we believe it best measure the
245 stopping behaviour of an individual (52). Indeed, the subsequent trials might reflect the inhibitory
246 learning of the individual and is investigated in a different study (53).

247

248 Behavioural measures of response inhibition tasks

249

250 For each quail, the dependent measures evaluated were (1) trial performance (i.e., whether
251 the trial was a success), and (2) time spent 'interacting' with the barrier/cylinder (i.e., time the bird
252 spends actively and repeatedly pecking/pushing the barrier).

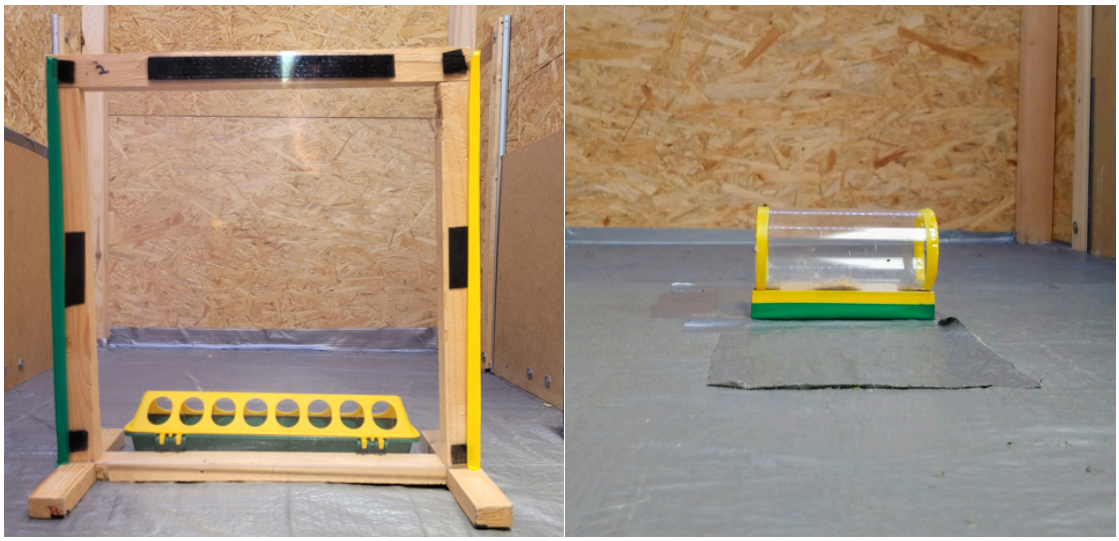


Figure 1. Apparatuses used for the *Barrier task* (left) and for the *Cylinder task* (right) with Japanese quails (n = 120).

Impulsive aggression tasks

Familiar Group

Apparatus. A feeder, identical to the one present in the home enclosure of individuals and filled with grains, was placed in the middle of the text box. A sheet of semi-transparent plastic was placed inside the feeder to control access to the food. The feeder was present through the duration of the trial, but access to the food was adjusted during the trial (see Procedures).

Procedures. Five quails from the same enclosure were tested together for two trials on two consecutive days. The five individuals were placed in the start box and, following the same procedure as during the previous tasks, were let into the test box after 15 seconds after the opaque door of the start box was removed. Trials lasted 10 minutes. During the first trial, access to the feeder was completely thwarted for the first five minutes of the trial (No Food phase), then partially thwarted so that only one individual could access the food for the last five minutes of the trial

(Limited Access phase). During the second trial, the procedure was reversed (i.e., Limited Access phase during the first five minutes, No Food phase during the last five minutes).

The same set of five birds were tested in the task. Repeated trials and different experimental phases allowed us to investigate whether quails' aggressive behaviour was repeatable across contexts differing in food availability. This aspect is being investigated in a different project and not analysed in this study (Vernouillet et al. in prep.). Here, we focused on the behaviour of individuals during the first trial in this study.

Unfamiliar Individual

Apparatus. Similar to the Familiar Group task, a feeder, identical to the one present in the home enclosure of individuals and filled with grains, was placed in the middle of the test box. A sheet of semi-transparent plastic was placed inside the feeder to control access to the food. The feeder was placed inside the test box during the trial (see Procedures).

Procedures. Two quails from a different enclosure and loft (but of the same experimental condition) were tested together for three trials on three consecutive days. Two individuals in the start box, and following the same procedure as during the precedent tasks, were let into the test box after 15 seconds from removing the opaque door of the start box. Trials lasted three minutes. The feeder was placed in the test box after one minute. During the first trial, only one bird had access to food when the feeder was placed in the test box. During the second trial, both birds could freely access the food when the feeder was placed in the test box. During the third trial, none of the birds had access to the food, as access was thwarted.

The same set of two birds were tested for each trial in the task. Repeated trials and different experimental phases allowed us to investigate whether quails' aggressive behaviour was repeatable across contexts differing in food availability. This aspect is being investigated in a different project

296 and not analysed in this study (Vernouillet et al. in prep.). Here, we focused on the behaviour of
297 individuals during the first trial in this study.
298
299 Behavioural measures of impulsive aggression tasks
300 For each quail, the dependent measures evaluated were (1) number of pecks given, (2)
301 number of pecks received, (3) time spent chasing, (4) time spent escaping, and (5) time spent
302 pushing. Descriptions of each behaviour can be found in Table S1.
303
304 *Statistical analyses*
305
306 We first wanted to perform a structural equation modelling approach (SEM) to determine
307 whether response inhibition, as estimated by the measures assessed during the Barrier and the
308 Cylinder tasks, could predict impulsive aggression, as estimated by the behavioral measures
309 assessed during the Familiar Group and the Unfamiliar Individual tasks. However, a preliminary
310 Confirmatory Factor Analysis indicated a lack of correlations among measures assessing the latent
311 factors of interest (i.e., response inhibition and impulsive aggression), and none of the models
312 tested had a decent fit (see Supplementary Material, Figures S2 and S3, Table S2 for more details
313 on factors analyses and SEM).
314 We thus used a different approach for our analyses. Importantly, unlike the SEM approach,
315 this approach does not allow us to infer the direction of the potential link between response
316 inhibition and impulsive aggression. First, to determine whether both the Barrier task and the
317 Cylinder task were assessing the same aspect of response inhibition, we correlated (1) first trial
318 performance using a tetrachoric correlation (for binary data), and (2) time spent 'interacting' with
319 the barrier/cylinder using a Pearson's correlation. Second, to determine whether both impulsive
320 aggression tasks were assessing the same aspect of aggression, we conducted a PCA with (1)
321 number of pecks given, (2) number of pecks received, (3) time spent chasing, (4) time spent

322 escaping, and (5) time spent pushing for both tasks. PCA was based on a correlation matrix. We
323 only considered components whose Eigenvalues were higher than 1 and for each component, we
324 only considered loadings whose contribution was higher than what was expected if all loadings
325 were of equal weight. Third, as we did not find any significant correlation between the different
326 response inhibition variables (see Results), we assessed whether higher levels of impulsive
327 aggression were linked to response inhibition deficits by evaluating whether aggression scores (as
328 calculated during the PCA) significantly differ between individuals that were successful during the
329 first trial of each response inhibition task using a Student t-test and whether they correlated with
330 time spent 'interacting' with the barrier/cylinder using a Pearson's correlation.

331 To determine whether early-life social environment influenced an individual's response
332 inhibition and/or impulsive aggression, we used a generalized linear model (GLM) approach, with
333 (1) trial performance (i.e., whether the barrier/cylinder testing trial was successful) for each
334 response inhibition task separately, and (2) time spent 'interacting' with the barrier/cylinder (i.e.,
335 time the bird spends actively and repeatedly pecking/pushing the barrier) for each response
336 inhibition task separately, as dependent variables associated with response inhibition, and (3) using
337 the PCA scores obtained for the first two axes, as aggressive behaviours during the Unfamiliar
338 Individual task mostly loaded on PC1 and aggressive behaviours during the Familiar Group task
339 mostly loaded on PC2 (see Results) as dependent variables associated with impulsive aggression.
340 Full models included social group condition, as well as morphological factors such as body weight
341 and sex.

342 To assess whether specific factors influenced our dependent variables, we compared full
343 models to a reduced model that did not include the factor that was evaluated (following the
344 procedures described by (54,55)). Parameter estimation was achieved using the residual maximum
345 likelihood ratio test.

346 For trial performance during the Barrier and the Cylinder tasks, we used a binomial
347 distribution. For time spent interacting with the barrier/cylinder, we rounded the values to the

348 nearest second and used a Poisson distribution. We first checked the assumptions of the GLMs
349 were met using the *DHARMa* package (56). Models were checked for dispersion and zero-inflation
350 using residual plots. In case residuals were over-dispersed, we added a dispersion parameter (this
351 was the case for the GLM on the second impulsive aggression score). In case there were too many
352 zero in our dataset, we added a zero-inflated model with a constant at the origin, and in the case
353 that the assumptions of the models were still not met, we changed the family to a negative binomial
354 family (this was the case for the GLM on time spent pecking for both response inhibition tasks).
355 Analyses were conducted using R version 4.3.2 (57) with the *glmmTMB* (58), *psych* (59),
356 *FactoMine*R (60), and *factoextra* (61). Descriptive statistics were obtained using the *Rmisc* package
357 (62). Plots were created using the *ggplot2* (63), *ggsignif* (64), *ggpubr* (65), *patchwork* (66), *wesanderson* (67)
358 packages. Alpha was set at 0.05 for all statistical analyses. All statistical analyses were performed by
359 AV, verified by KW and CAT.
360

361 **4. Results**

362

363 *Overview of response inhibition tasks*

364

365 Overview of Barrier task

366

367 During the testing trial, 19 individuals detoured successfully (i.e., without touching the
368 transparent barrier), 93 individuals detoured unsuccessfully (i.e., after touching the transparent
369 barrier), seven individuals touched the barrier but did not detour during the entire duration of the
370 trial, and one did not interact with the apparatus nor detoured around the transparent barrier (view
371 Table S3 for an overview of the response outcomes of the quails based on their social group and
372 on sex). Among individuals who pecked the barrier (n = 100), average time spent pecking the
373 barrier was 17.5 (±*SE*: 1.4) seconds.

374

375 Overview of Cylinder task

376

377 During the first testing trial, 14 individuals detoured successfully (i.e., without touching the
378 transparent cylinder), 46 individuals detoured unsuccessfully (i.e., after touching the transparent
379 cylinder), 36 individuals touched the cylinder but did not detour, and 24 did not interact with nor
380 detoured around the cylinder (view Table S3 for an overview of the response outcomes of the
381 quails based on their social group and on sex). Among individuals who pecked the cylinder (n =
382 82), average time spent pecking the cylinder was 15.0 (±*SE*: 1.6) seconds.

383

384 Repeatability of response inhibition

385

There were 88 individuals who were not successful during either response inhibition task, 18 individuals who were successful during the Barrier task only, 13 individuals who were successful during the Cylinder task only, and only one individual who was successful during both response inhibition tasks.

For this analysis, only individuals who interacted (either by detouring around and/or by pecking the transparent barrier) during both tasks were included (n = 95). Results from the correlations indicated that both tasks were measuring different aspects of RI, as neither performance between tasks (tetrachoric correlation coefficient: -0.250) nor time spent interacting with the transparent barrier/cylinder (Pearson's correlation: t = -1.129, df = 93, p = 0.262, Fig. 2) correlated between tasks.

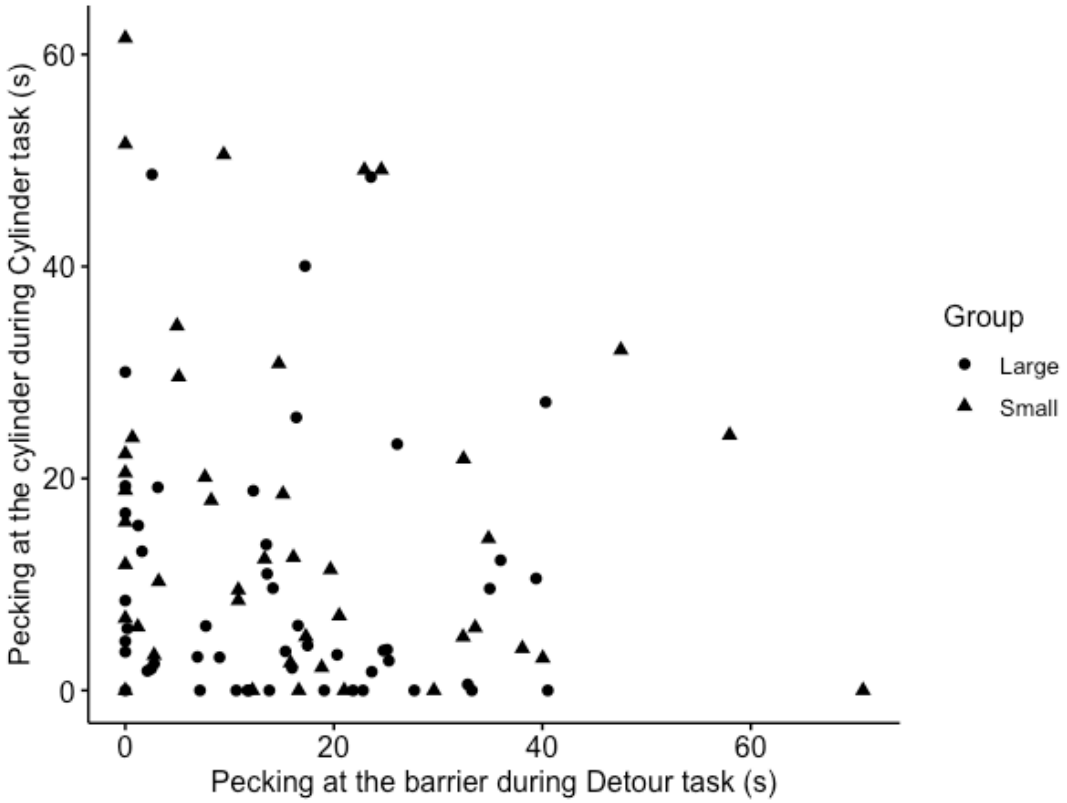


Figure 2. Time spent pecking at the transparent barrier during the Barrier task did not significantly correlate with the time spent pecking the cylinder during the Cylinder task in Japanese quails (Pearson's correlation: t = -1.129, df = 93, p = 0.262).

401

402 *Overview of impulsive aggression tasks*

403

404 Overview of Familiar Group task

405

406 All 120 individuals participated during the Familiar Group task. Quails gave on average 8.2
407 ± 16.7 pecks, received on average 8.2 ± 9.0 pecks, chased another individual for 1.0 ± 5.0 seconds,
408 escaped for 1.7 ± 4.4 seconds, and pushed others for 2.3 ± 6.0 seconds.

409

410 Overview of Unfamiliar Individual task

411

412 All 120 individuals participated during the Unfamiliar Individual task. Quails gave on
413 average 2.5 ± 5.3 pecks, received on average 2.5 ± 5.3 pecks, chased another individual for 1.8 ±
414 5.7 seconds, escaped for 3.3 ± 7.5 seconds, and pushed the other for 0.3 ± 0.9 seconds.

415

416 Repeatability of impulsive aggression

417

418 All individuals were included in the analysis, as they all participated in both tasks (n = 120).
419 Results of the PCA indicated that there was not a unique impulsive aggression aspect measured
420 during the tasks.

421 The first five components had an Eigenvalue higher than 1 and together explained 78.1 %
422 of the variance in the data. The first component explained 21.7 % of the variance, the second
423 component explained 18.6 % of the variance, the third component explained 14.8 % of the variance,
424 the fourth component explained 12.5 % of the variance, and the fifth component explained an
425 additional 10.5 % of the variance.

426 Additionally, we found that both tasks investigated a different impulsive aggression aspect,
427 as measures related to each task loaded on different components (Table 1). Interestingly, number
428 of pecks given, amount of time spent chasing, and amount of time spent pushing loaded on the
429 opposite of number of pecks received and amount of time escaping on the two first components,
430 suggesting that individuals engaging in aggressive behaviors were receiving aggressive behaviors
431 from other individuals.
432
433 Table 1. PCA loadings for the measures on impulsive aggression in Japanese quails. Loadings
434 considered important (i.e., whose contribution was higher than what was expected if all loadings
435 were of equal weight) are indicated in bold.
436

		Dimensions				
		1	2	3	4	5
Familiar Group	Number of pecks given	0.044	**-0.737**	**0.440**	0.176	0.186
	Time spent chasing	0.148	**-0.644**	0.191	0.300	**0.530**
	Time spent pushing	-0.036	-0.264	**0.606**	0.070	**-0.626**
	Number of pecks received	0.254	**0.563**	**0.488**	0.020	0.310
	Time spent escaping	**0.483**	**0.509**	0.128	0.082	**0.346**
Unfamiliar Individual	Number of pecks given	**0.716**	-0.036	-0.271	**0.457**	-0.148
	Time spent chasing	**0.493**	-0.183	**-0.553**	**0.382**	-0.170
	Time spent pushing	**0.515**	0.310	**0.491**	0.279	-0.264

	Number of pecks received	**-0.624**	0.280	0.058	**0.599**	-0.010
	Time spent escaping	**-0.662**	0.211	-0.059	**0.574**	0.053

For the subsequent analyses, we used the individual scores obtained on the first two components, as they best represent the aggression scores during each task (PC1 for Unfamiliar Individual, PC2 for Familiar Group).

Relationship between response inhibition and impulsive aggression

We evaluated whether the different response inhibition behavioural measures were related to the aggression scores of the individuals. For these analyses, we used reduced datasets that included quails that interacted with the apparatuses (either by detouring successfully or by pecking at the apparatus) either during Barrier task (n = 119) for measures associated to that task or during the Cylinder task (n = 96) for measures associated to that task.

Aggression scores for the Unfamiliar Individual task (PC1) significantly correlated with the amount of time spent pecking on the cylinder during the Cylinder task, with individuals that spent more time pecking at the cylinder having a higher aggression score than individuals that spent less time pecking at the cylinder (t = 2.199, $d.f.$ = 94, p = 0.030; Fig. 3) and tended to be higher in unsuccessful individuals in comparison to successful individuals (t = 2.072, $d.f.$ = 18.08, p = 0.053). Response inhibition measures assessed during the Barrier task did not significantly explain the aggression scores for that task (Performance during the Barrier task: t = -0.090, $d.f.$ = 38.55, p = 0.929; Time spent pecking the transparent barrier: t = -0.197, $d.f.$ = 117, p = 0.844).

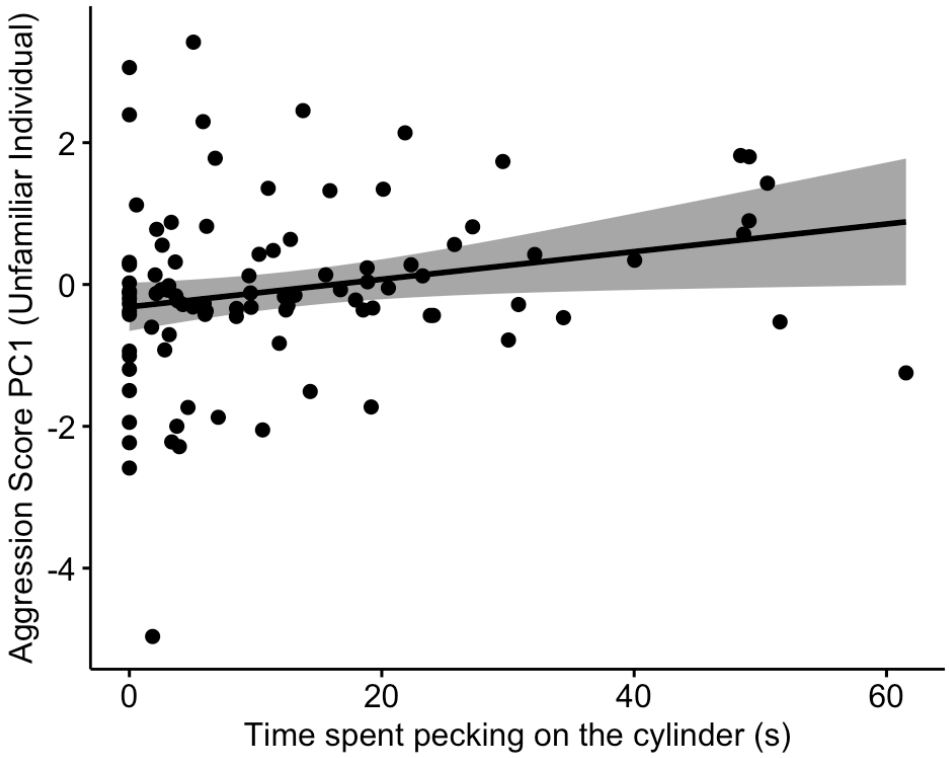


Figure 3. Time spent pecking on the cylinder during the Cylinder task significantly predicted the aggression scores obtained during the Unfamiliar Individual task.

Aggression scores for the Familiar Group task (PC2) were significantly linked to the performance during the Barrier task, with individuals that successfully detoured during the Barrier task being more aggressive than individuals that were unsuccessful (t = 2.757, $d.f.$ = 20.79, p = 0.012; Fig. 4). No other response inhibition measures significantly influenced the aggression scores for this task (Performance during the Cylinder task: t = 1.588, $d.f.$ = 20.54, p = 0.128; Time spent pecking the transparent barrier: t = -1.757, $d.f.$ = 117, p = 0.082; Time spent pecking the transparent cylinder: t = -1.645, $d.f.$ = 94, p = 0.103).

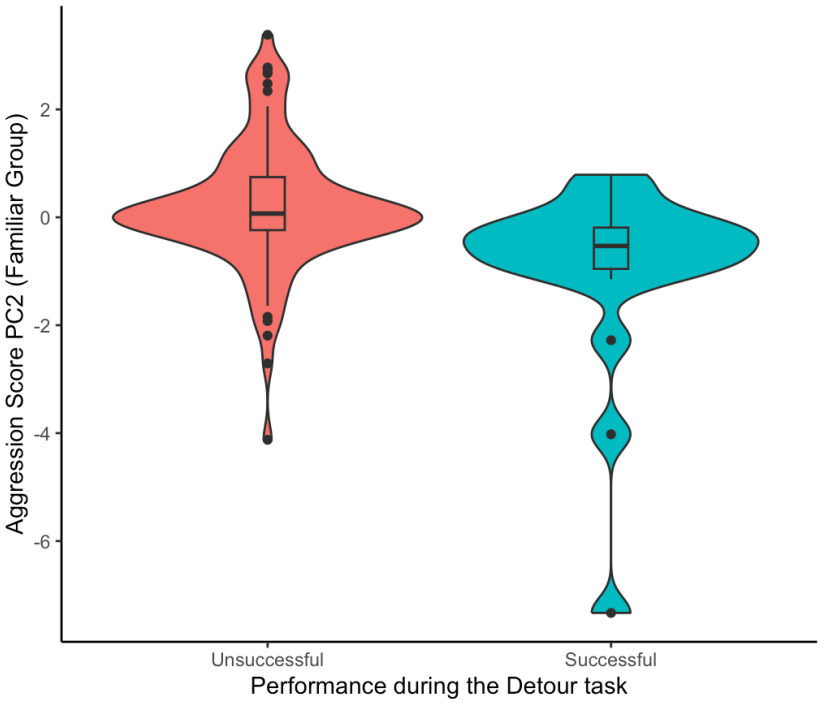


Figure 4. Performance during the Barrier task significantly predicted the aggression scores obtained during the Familiar Group task. Note that for this aggression score, negative scores indicate more aggressive behaviours than positive scores.

Influence of group size on response inhibition and impulsive aggression

<u>Influence of Group size on response inhibition</u>

Given the lack of contextual repeatability, we evaluated the effects of Group Size, Sex, and Body Weight on performance and on the time spent interacting with the transparent barrier/cylinder for both Response Inhibition tasks separately.

Only individuals who interacted (either by detouring around and/or by pecking the transparent barrier) were included for the analyses on performance (n = 119 for the Barrier task, n = 96 for the Cylinder task; see Table S3 for overview of number). Performance during the Barrier

task and performance during the Cylinder task were not explained by Group Size, Sex, nor Body Weight (Table 2).

Table 2. Factors evaluated to explain performance during the Barrier task (n = 119 quails) and during the Cylinder task (n = 96 quails).

	Performance Barrier task			Performance Cylinder task		
	χ^2	*d.f.*	*p*	χ^2	*d.f.*	*p*
Group Size	0.732	1	0.392	0.421	1	0.517
Sex	3.725	1	0.054	1.410	1	0.235
Body Weight	1.298	1	0.255	0.002	1	0.965

Only individuals who pecked at the transparent barrier were included for the analyses on time spent pecking (n = 100 for the Barrier task, n = 82 for the Cylinder task; see Table S3 for overview of number). Time spent pecking at the transparent barrier during the Barrier task was not explained by Group Size (χ^2 = 1.608, *d.f.* = 1, p = 0.205; Fig. 5) nor by Sex (χ^2 = 0.063, *d.f.* = 1, p = 0.802). However, Body Weight significantly influenced time spent pecking at the transparent barrier, with individuals with a lower weight spending more time interacting with the barrier than individuals with a higher weight (χ^2 = 5.835, *d.f.* = 1, p = 0.016; Fig. S4).

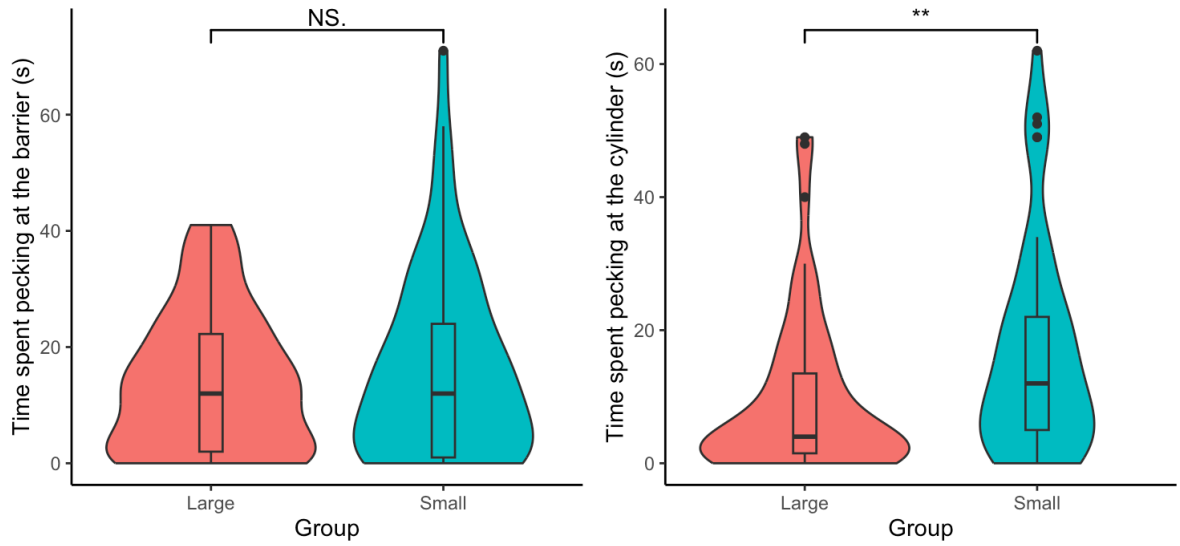


Figure 5. Left. Time spent pecking at the transparent barrier during the Barrier task did not significantly differ between social groups (χ^2 = 1.608, *d.f.* = 1, p = 0.205). Right. Quails in the Large group spent significantly less time pecking at the transparent cylinder than quails in the Small group (χ^2 = 6.256, *df* = 1, p = 0.012).

Group Size significantly influenced the time spent pecking at the transparent cylinder during the Cylinder task, with individuals in the Large group spending less time pecking at the transparent cylinder than individuals in the Small group (Time spent pecking at the transparent cylinder $M \pm SE$: Large group: 11.64 ± 1.92 s, Small group: 18.70 ± 2.50 s; χ^2 = 6.256, *df* = 1, p = 0.012; Fig. 5). Body Weight also significantly influenced time spent pecking at the cylinder, with individuals with a higher weight spending more time interacting with the cylinder than individuals with a lower weight (χ^2 = 14.268, *d.f.* = 1, p < 0.001; Figure S4). There was no significant difference between males and females (χ^2 = 3.719, *d.f.* = 1, p = 0.054).

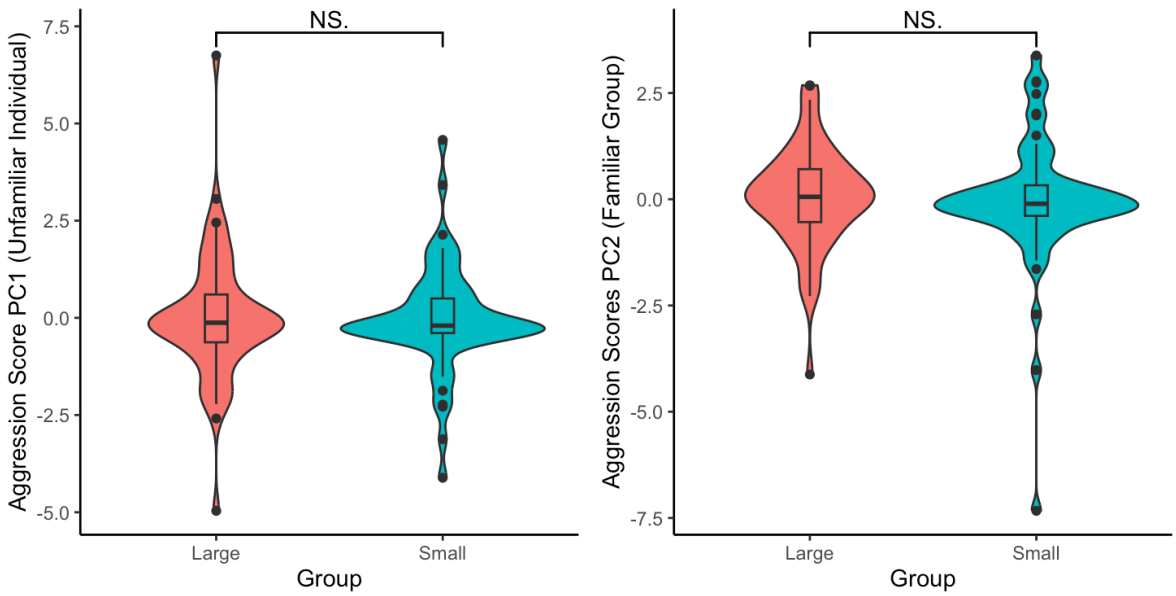
<u>Influence of Group size on impulsive aggression</u>

517 Given the lack of repeatability in impulsive aggression between contexts, we evaluated the
518 effects of Group Size, Sex, Body Weight on the aggressive scores for both impulsive aggression
519 tasks separately (n = 120 quails).

520 Aggression scores for the Unfamiliar Individual task (PC1) were not explained by Group
521 Size (χ^2 = 0.001, *d.f.* = 1, p = 0.973; Fig. 6) nor by Body Weight (χ^2 = 1.178, *d.f.* = 1, p = 0.278).
522 However, male quails had a significantly higher aggression score than female quails (Females: -0.28
523 ± 1.54, Males: 0.28 ± 1.38; χ^2 = 4.318, *d.f.* = 1, p = 0.038; Figure S5).

524 Aggression scores for the Familiar Group task (PC2) were not explained by Group Size (χ^2
525 = 0.183, *d.f.* = 1, p = 0.670; Fig. 6). However, males were significantly more aggressive than females
526 (Females: 0.35 ± 0.97, Males: -0.35 ± 1.61; χ^2 = 8.554, *d.f.* = 1, p = 0.004; Figure S5), and quails
527 with a higher weight were significantly more aggressive than quails with a lower weight (χ^2 = 6.002,
528 *d.f.* = 1, p = 0.016; Figure S6).

529



530

531 Figure 6. There were no significant differences in aggression scores between social groups a) during
532 the Unfamiliar Individual (χ^2 = 0.001, *d.f.* = 1, p = 0.973), and b) during the Familiar Group task

533 ($\chi^2 = 0.183$, $d.f. = 1$, $p = 0.670$). *Note: for the axis PC2, more aggressive individuals have a negative

534 score.

535

536

537

538 **5. Discussion**

539

540 The main goals of this study were threefold: (A) to examine the link between response
541 inhibition and impulsive aggression at an individual level, and (B) to assess whether group size
542 during early-life environment influenced the development of response inhibition and (C) impulsive
543 aggression. We found (A) some significant correlations between measures of response inhibition
544 and impulsive aggression, providing some limited support to the theoretical model linking both
545 concepts. We also found (B) evidence that early-life social environment indeed shapes the
546 development of response inhibition, as quails raised in smaller social groups spent more time
547 repeating an inefficient action (i.e., pecking at the cylinder) than those raised in larger social groups.
548 However, contrary to what we expected, (C) we found no evidence that early-life social
549 environment influenced the development of impulsive aggression.

550

551 *Relationship between response inhibition and impulsive aggression*

552

553 In Japanese quails, we found some evidence that response inhibition was significantly linked
554 to impulsive aggression at an individual-level. More specifically, increased perseveration on an
555 unrewarded action towards an unfamiliar object (i.e., time spent pecking at the transparent cylinder)
556 was significantly correlated to increased aggression towards unfamiliar individuals. This result may
557 suggest that individuals tend to interact aggressively towards novelty, be it an object or an individual.
558 The link between higher aggression and lower inhibition has also been found in previous
559 observational studies in mammals (12,13,68,69), as suggested by theoretical models (14). In
560 primates, aggressive individuals with low response inhibition are thought to have an advantage to
561 access and retain food resources (70). A similar observation was found in Australian magpies, where
562 individuals involved in aggressive interactions (both initiating and receiving) performed worse in
563 an associative learning task, possibly due to lower time and/or energy to attend the task (71). While

564 the authors did not test inhibition directly, previous work in that study population has found a
565 significant correlation between inhibition (as assessed with a cylinder) and associative learning (31).
566 Together, these results highlight how the social environment, its dynamics, and cognitive
567 performance are tightly linked with one another.

568 Interestingly, we also found that individuals that successfully fully cancelled a discrete action
569 (i.e., by detouring without pecking at the transparent barrier) had significantly increased levels of
570 aggression towards familiar individuals. This result goes in the opposite direction to what we
571 predicted, and contrast with previous studies that investigated the link between inhibition and
572 aggression. One potential explanation for this seemingly contradictory result could be by viewing
573 the adaptive significance of aggression (3). Indeed, aggressive individuals are more likely to initiate
574 contests and to subsequently win them (72), which potentially gives them higher fitness payoffs.
575 Hence, individuals with better response inhibition may use the most advantageous coping strategy
576 in response to the social environment demands.

577 These contradictory results may suggest three things: a) that the mechanisms involved during
578 the cancellation of an action may depend on whether the individuals are already engaged in the
579 action they need to inhibit, and/or b) that the tasks are not assessing response inhibition or
580 aggression, but rather pecking tendency (whether it is towards an object or an individual), and/or
581 c) that response inhibition and aggression depends highly on the social context.

582 Indeed, when examining in detail the requirements of both the Detour and the Cylinder tasks,
583 we observe that individuals may have to inhibit two actions: first, the prepotent response of going
584 directly at the food, thus pecking at the transparent barrier, and second, the repetitive action of
585 pecking along the barrier if they failed to inhibit the first action (73). Not only the nature of the
586 action to be stopped, but the overall task context in which actions need to be stopped could thus
587 involve different mechanisms.

588 The lack of correlations between the different measures of the two response inhibition tasks
589 we observed is consistent with results from previous studies who have used the same tasks (e.g., in

590 dogs: (52,74,75); in pheasants: (76)). This occurred despite both tasks having similar task demands
591 in general (i.e., detouring tasks requiring individuals to detour around a transparent barrier, (47))
592 and despite both tasks having a similar "go" stimulus (i.e., the visible food reward) and a similar
593 "stop" stimulus (i.e., the transparent barrier) present at the same time (for a recent in-depth
594 discussion about the importance of the "go" and 'stop" stimuli in response inhibition tasks, please
595 refer to (73)). Rather, the characteristics of the stop stimulus itself, such as the shape (e.g., (77))
596 and the motor action required to successfully detour, might influence the individual's response: the
597 transparent barrier in the Barrier task is large and requires individuals to move their entire body
598 around it, whereas the transparent barrier in the Cylinder task is small and requires individuals to
599 place their head through the openings (52).

600 Alternatively, the lack of repeatability in performance might be due to training differences.
601 Indeed, for the Barrier task, individuals were trained to go around the opaque barrier and might
602 have learned the detouring solution (78), explaining the high success of individuals in this task
603 during the testing trial. In comparison, individuals were not trained during the Cylinder task. Hence,
604 during the Cylinder task, individuals must not only learn to inhibit pecking at the transparent
605 cylinder, but also to successfully "solve" the task (52). This may also explain why the number of
606 individuals who successfully detoured during the Cylinder task was lower than the ones who did
607 during the Barrier task.

608 Interestingly, the lower detouring performance during the Cylinder task, i.e., the second
609 testing trial involving detouring around a transparent barrier, suggest that individuals were unable
610 to use their previously experience of detouring around a transparent barrier in a different context.
611 Unlike what was found with pheasants by van Horik et al. (76), quails did not learn to inhibit
612 interacting with a transparent surface between the two tasks, as the duration of pecking at the
613 transparent surface did not differ between tasks. However, we found evidence that Japanese quails
614 did learn to inhibit pecking with repeated trials during the Cylinder task (53).

615 Even when carefully choosing tasks purporting to assess the same aspect of response
616 inhibition, there is a lack of repeatability in an individual's behavioural response. Understanding
617 how and why exactly there is such a low reliability between tasks is beyond the scope of the current
618 study but warrants further investigation (79). Yet, together, these results suggest that, despite using
619 similar tasks, response inhibition is multi-faceted and highly dependent on the action that needs to
620 be stopped and/or on the context in which stopping need to occur.

621 Similarly, the contradictory results we obtained regarding the link between aggression and
622 response inhibition may be due to the contextual differences between both aggression tasks. The
623 lack of repeatability in individual aggression scores is surprising as it goes against the idea of
624 aggression as a personality trait (e.g., (80–82)). Instead, this result suggests that aggression is subject
625 to high intra-individual variation (83). Plasticity in aggressive responses could depend on the
626 outcome of past antagonistic interactions (84) and on the traits of the other individual, such as
627 status signals or signals of fighting ability (reviewed by (85)) or use social information to assess the
628 costs of engaging in an antagonistic behaviour towards another individual (86). Individuals'
629 behaviour may also differ when they are in the presence of familiar and of unfamiliar individuals
630 (e.g., (87), "winner and loser effects" – (88), "dear enemy" hypothesis – as reviewed by (89); but
631 see (44) for a counter-example with male Japanese quails). Indeed, because agonistic interactions
632 between individuals can be costly, familiarity is thought to play a key role in the formation of
633 hierarchies, both within species (90) and between species (91). For this reason, aggression is usually
634 reduced within the group once hierarchies are established (3). Regardless of the lack of correlations
635 in aggressive behaviours between tasks, we found that behaviours associated with individuals that
636 were the target of aggressive behaviours (as assessed by the time spent escaping and the number
637 of pecks received) were less likely to engage in aggressive behaviours (as assessed by the time spent
638 chasing and pushing, and the number of pecks given) in each task context.

639 Finally, another methodological aspect that may explain this duality in our results linking
640 response inhibition and aggression is the use of food rewards in a group context during the

641 aggression tasks and in a solitary context during the response inhibition tasks. Indeed, the social
642 context may exert different inhibitory pressures on individuals, despite having similar motivation
643 levels in both cases. For instance, in the presence of a more dominant or more aggressive group
644 member, an individual might inhibit going towards the food reward to reduce the risk of receiving
645 directed aggression (92). However, when alone, that same individual may or may not have lower
646 response inhibition levels towards the food rewards. This possibility suggests, once again, the
647 importance of accounting for the social context when evaluating impulsivity.

648 In sum, we found evidence that response inhibition is linked to impulsive aggression. But
649 given that the relationship is not as clear cut as we expected and that we were unable to assess the
650 direction of that relationship due to the lack of correlations between tasks, our conclusions
651 regarding the link between the two are not as definitive as we had hoped them to be. For instance,
652 we cannot exclude the possibility that other factors might mediate the relationship between the
653 two (19) nor can we definitely say that aggression results from deficits in response inhibition. Next,
654 we explored whether social environment during early life might contribute to deficits in response
655 inhibition and/or to impulsive aggression.

656

657 *Influence of early-life social environment on response inhibition and impulsive aggression*

658

659 The importance of the social environment on the development of cognition has been
660 suggested in many species (20,21,23,30,71,93). More specifically, social group size, a key
661 component of the social environment, usually correlates with higher levels of inhibition in hyenas
662 (32) and in Australian magpies (31), but not in guppies (34,94) nor in horses (95). Here, we found
663 that quails raised in larger groups inhibited a repetitive unrewarded action (i.e., pecking at the
664 transparent cylinder) faster, on average, than quails raised in smaller groups. This result aligns with
665 those from previous studies evaluating intraspecific variability in response inhibition using the
666 Cylinder task on Australian magpies and on hyenas (31,32), and support what we predicted.

667 However, we found no significant effect of social group size on the overall performance for both
668 tasks, nor on the time spent pecking on the transparent barrier during the Barrier task. As we
669 previously mentioned, both tasks may not measure the same aspect of response inhibition or may
670 measure pecking tendency in one or the other. Therefore, the influence of the social environment
671 might be mediated differently depending on which aspect of response inhibition is considered.

672 Early-life social environmental conditions have strong effects on aggressive behaviour in
673 many species, including birds (96), farm animals (97), and humans (e.g., (42)), with usually a
674 decrease in aggression as group size increases. For quails specifically, they are more aggressive when
675 they are raised in social isolation than when they have been raised with others (98). Unlike previous
676 research, we found no significant difference in levels of aggression between groups during our
677 aggression tasks. Hence, we found no evidence that quails become more socially tolerant with
678 increasing group size (e.g., (37,40,49)), even if admittedly we did not assess the aggression
679 experienced by individuals outside of the experimental context. However, this lack of significant
680 results might be caused by the increase in density associated with the increase in group size, as
681 individuals of both conditions were given the same size enclosure. Higher population density has
682 been associated with higher aggression levels (e.g., lizards – (99)). Hence, in our study, the potential
683 reduction in aggression due to group size might be confounded with increase in aggression due to
684 increase in density and might have switched to a resource defense strategy instead. A next step is
685 to disentangle the effects of group size and group density on aggression as well as on response
686 inhibition. Alternatively, differences in social group size can have affected social motivation (i.e.,
687 the motivation to seek proximity with other group members) and social bonding in quails. Indeed,
688 Japanese quails raised in larger social group show less positive social interactions (100), potentially
689 because their ability to recognize familiar individuals and remember past interactions with them
690 decrease as the number of group members increase (30).

691 Social group size is not the only aspect of social complexity. Group dynamics and stability,
692 as well as the nature of the relationships between group members, are other important aspects that

693 contribute to the variation in social complexity within and between groups (29). Further
694 investigation is needed to determine which aspects of the social life influence the development of
695 aggression and of response inhibition.
696
697 *Intra- and inter-individual variation in response inhibition and in impulsive aggression*
698
699 Research on non-human animals had, until recently, tried to minimize the importance of
700 inter-individual variation in cognition (101,102). Now, there is a general effort in pinpointing which
701 factors may underlie individual differences in cognition generally (103,104). Indeed, despite
702 controlling the early-life physical and social environment of our quails, as well as the acclimatation,
703 habituation and testing procedures, we still observed pronounced individual differences in
704 performance and in the time spent performing a repetitive unrewarded action during the response
705 inhibition tasks and in the aggressive behaviours during the impulsive aggression tasks that were
706 not explained by the difference in group size. Here, we can only speculate about the causes of these
707 differences in our sample.
708 Inter-individual differences in response inhibition and impulsive aggression, as well as the
709 lack of repeatability across tasks, may be due to differences in motivation and attention (105,106).
710 Once again, despite controlling the food deprivation procedure to ensure similar motivation to
711 participate in each task, some individuals might have greater motivation than others, due to higher
712 basal energetic demands (107) or lower availability of food in their home enclosure (108). This
713 might also explain why we found an effect of body weight on time spent pecking at the transparent
714 barrier (also found in New Zealand robins, (109)). However, given that the direction of that effect
715 was opposite for both response inhibition tasks, we cannot confirm this explanation as to why or
716 how it might be the case. Additionally, in group-living domestic species, more aggressive individuals
717 often outcompete less aggressive individuals for limited resources and have a higher weight as a
718 result (e.g., (110)), which support our findings on heavier individuals being more aggressive towards

719 familiar individuals. Concurrently, being aggressive might be less costly and more beneficial for
720 larger individuals, as they are more likely to physically outcompete smaller ones.

721 Cognitive abilities and personality traits have also been known to differ between females and
722 males (111). Previous work on mosquitofish (112), baboons (113), dogs (114), and guppies (115),
723 has shown that females are significantly better than males at inhibiting their responses. Yet this was
724 not the case in our quails nor in other species tested, such as Australian skinks (107), spotted
725 hyaenas (32), gulls (73), and red junglefowls (116). Despite not finding any differences in response
726 inhibition between males and females, we found that males were significantly more aggressive than
727 females. Indeed, early studies suggest that most aggressive behaviors are initiated by sexually mature
728 males towards other males and females (117). For this reason, sexually experienced females tend
729 to avoid relatively aggressive males (118), as cohabitation with aggressive males lead to increased
730 baseline cortisol levels (119), lower egg quality (120), and lower plumage quality (44), amongst
731 others. Aggressive behaviors can also be initiated by sexually mature females when paired with an
732 unfamiliar individual (both males and females), but their aggression rates decreased quickly over
733 time, which was not the case for males (121). Here, interestingly, we found such a sex difference in
734 aggression when the quails were between 5- and 6-weeks old, at the onset of sexual maturity in
735 Japanese quails (between 6- to 8-weeks old). Little is known regarding aggression in immature, non-
736 sexually active or castrated quails, but it is usually assumed they have lower aggressive tendencies
737 than sexually mature ones (43,122). Hence, inter-individual variation in aggression that we observed
738 might also be due to inter-individual differences in reaching sexual maturity, despite keeping all
739 other parameters constant for all individuals (photoperiod, temperature, food).

740 Personality traits, especially neophobia (i.e., the fear to interact with novelty) and exploration
741 (i.e., the willingness to interact with novelty, (123)) have also been suggested to explain differences
742 in cognitive abilities ((124), also reviewed in (125)), or even the motivation to participate in the
743 tasks or interact with the apparatuses (e.g., self-selection by participation of less neophobic
744 individuals in the population, (126,127)). To a lesser extent, neophobia and exploration could also

745 explain some inter-individual behavioural differences we observed during the aggression tasks, as
746 less neophobic and/or more exploratory individuals might approach unfamiliar individuals and
747 interact with them. For instance, more exploratory great tits (*Parus major*) are more likely to initiate
748 fights (128). Yet, whether personality traits derive from cognitive abilities, or *vice versa*, remains
749 debated in the field of animal cognition (and even between the authors of the current paper).

750 Finally, a large inter-individual variation might indicate a lack of strong selection on a given
751 trait. For instance, there was no evidence that response inhibition contributed to social rank,
752 foraging efficiency, or risk taking in red junglefowl females (116), suggesting that there might be a
753 lack of strong selection on response inhibition, potentially explaining why there is such strong
754 variation in response inhibition between individuals. Alternatively, a large inter-individual variation
755 in response inhibition within the population might indicate that inhibiting a behavioral response
756 might be favored in certain environments or contexts, but not in others (129,130). For example,
757 lower-ranked individuals, especially in large social groups, may benefit from having a higher level
758 of response inhibition, possibly to reduce conflicts with higher-ranked individuals (32). Similar
759 arguments can be made to explain intra-individual variation in response inhibition and in aggression.
760 Indeed, the lack of repeatability in response inhibition at an individual-level may suggest that
761 individuals are flexible in their cognitive ability and in their social behavior, depending on the
762 context. For instance, impulsive actions might be more adaptive in an unstable or unpredictable
763 environment or when travel time between resources increase (131). Understanding in which
764 contexts extreme values of response inhibition and if might be favored and why such variation in
765 cognitive traits and in personality exists within the population is a topic that warrants further
766 investigation.

767

768 **6. Conclusion**

769 In summary, our study provides one of the first experimental evidence that early-life social
770 environment can influence the development of response inhibition. We also experimentally

showed that certain aspects of aggression are linked to deficits in response inhibition, especially regarding perseverating in performing an unrewarded action towards novelty (objects and/or individual). Hence, our study shed some light regarding the mechanisms underlying impulsive aggression using Japanese quails. Yet, contrary to what was expected based on previous literature, group size, a key aspect of early-life social environment, did not influence aggression in our quails, despite it influencing certain aspects of response inhibition (the same ones that were linked to aggression). Aggression is a multifaceted and complex behaviour that involves multiple processes (132,133). Thus, despite controlling the physical and social environment, intrinsic factors such as genetics, motivation, non-social personality traits (i.e., neophobia, exploration, activity), and the ability to get social information might explain inter-individual variability in aggression that we witnessed and mediate the link between response inhibition and aggression. Regarding the influence of sociality on the emergence of aggressive behaviors, other social factors, such as group dynamics and stability, and further research is warranted to fully understand how sociality, response inhibition, and aggression relate to one another.

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Ethical Statement

The experiment was performed in accordance with the Association for the Study of Animal Behaviour ethical guidelines under permission of the ethical committee of animal experimentation (VIB Site Ghent, Universiteit Gent): EC2022-005.

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Data Accessibility

All videos of the experiment can be found on Zenodo (https://zenodo.org/records/13361318). R codes and extracted data from BORIS can be found on OSF (https://osf.io/2b5uy/).

Competing Interests

None to declare.

Author contributions

Based on the CRediT system, the contributions of the authors are as follow: 'Conceptualization' – AV, LL, FV; 'Data curation' – AV, KW; 'Formal analysis' – AV; 'Funding acquisition' – AV, AD, WZ, CAT, AM, LL, FV; 'Investigation' – AV, KW, RA, AD, WZ, CAT, SK, LL, FV, 'Methodology' – AV, KW, RA, AD, LL, FV; 'Project administration' – AV, FV; 'Resources' – FV, 'Supervision' – AV, LL, FV; 'Validation' – AV, KW, SK, CAT; 'Visualization' – AV, 'Writing—original draft' – AV, and 'Writing—review & editing' – AV, KW, RA, AD, WZ, CAT, AM, LL, FV. In the Methods section, we followed the MERIT system (Nakagawa et al. 2023).

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