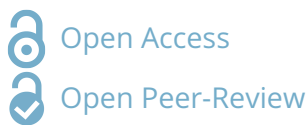


RESEARCH ARTICLE



1 **Do Ecological Valid Stop Signals Aid**
2 **Detour Performance? A**
3 **Comparison of Four Bird Species.**

Cite as:

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13 **Abstract**

Response inhibition, or the stopping of actions, is considered a key component of flexible and adaptive behaviour. Across fields, response inhibition is often treated as a unitary cognitive mechanism. However, we propose that response inhibition consists of a chain of cognitive processes, including the detection of a stimulus, the selection of an appropriate behaviour (go or stop), and the implementation of it (execution or inhibition of a motor response). Likewise, we propose that individual variation in response inhibition can arise at the early signal detection stage. Here we will test this idea in a detour barrier task, which is one of the most popular tools to study response inhibition in non-human animals. The role of signal detection in detour tasks has been largely neglected, with a few notable exceptions. We will therefore partially replicate two previous studies that manipulated the perceptual characteristics of the barrier, while addressing some conceptual and methodological shortcomings of the original work. Specifically, we will compare how detour performance of four bird species (i.e., white leghorn chickens, Japanese quails, herring gulls and domestic canaries) is differently influenced by vertical- and horizontal-barred barriers. Based on the previous work, we predict better detour performance when the perceptual characteristics of the barrier match the ecological niche of the species.

Keywords: Response Inhibition; Stop-Signal Detection; Comparative Approach; Birds; Detour

Introduction

Response inhibition (RI) refers to stopping or cancelling actions that are no-longer relevant, inappropriate, or overly risky (Verbruggen and Logan, 2008b, 2017). It is often regarded as a critical component of flexible and adaptive behaviour (Verbruggen and Logan, 2008b). For example, animals living in urban environments must often inhibit no-longer relevant behaviours when confronted with environmental conditions that differ significantly from their ancestral ones (Lee and Thornton, 2021); lower-ranked animals need to inhibit inappropriate, disobedient behaviour in the presence of dominant animals (Johnson-Ulrich and Holekamp, 2020); and foraging animals must refrain from approaching a food source when this action becomes overly risky due to the emergence of a predator (Tvardíková and Fuchs, 2012). These examples demonstrate that RI (or a lack thereof) can have important fitness consequences (e.g., the animals may be predated if they fail to stop foraging when the predator emerges).

One of the most popular tasks to study RI in animals is the detour task (Kabadayi, Jacobs, et al., 2017; Miller and Tallarico, 1974; Regolin, Giorgio, et al., 1995; Regolin, Vallortigara, et al., 1994; Van Horik, Beardsworth, Laker, Whiteside, et al., 2020; Van Horik, Langley, et al., 2018; Zucca, Antonelli, et al., 2005; Zucca and Sovrano, 2008). In this task, the direct path to a motivationally-salient stimulus (e.g., food or a social companion) is blocked by a barrier or cylinder. Animals have to inhibit their prepotent response to go directly for the reward (as the direct path is blocked), and instead make a detour around the barrier or cylinder to obtain the reward. Detour tasks have been used in non-human animals, such as birds, to study e.g., how the social or physical environment shapes RI. For example, wild Australian magpies (*Gymnorhina tibicen*) demonstrated superior detour performance when reared in large compared with small social groups (Ashton et al., 2018). Another study found that pheasants (*Phasianus colchicus*) showed superior detour performance when reared in spatially unpredictable compared with predictable environments (Van Horik, Beardsworth, Laker, Langley, et al., 2019). Combined, these findings suggest that RI development is facilitated in e.g., environments with high social demands or environments that promote the expression of diverse foraging strategies.

Typically, performance in the detour task has been linked to the variation in the effectiveness of a single cognitive control function, 'response inhibition', or more generally, 'inhibitory control' (which is an umbrella term for various types of inhibition, which may or may not be related to each other; Bari and Robbins, 2013). However, by referring to general ill-defined cognitive constructs such as RI (or even worse, a general umbrella term such as 'inhibitory control'), we do not explain the underlying cognitive mechanisms or building blocks of stopping (Verbruggen, McLaren, et al., 2014), as the explanation is 'just as mysterious as the thing it is supposed to explain' (Press et al., 2022). To address this issue in the human RI literature, a theoretical framework of RI has been proposed (Verbruggen, McLaren, et al., 2014). Based on empirical work in humans, primates, and rodents, the authors of the framework proposed that RI involves a chain of processes. More specifically, RI would involve at least three basic processes: the detection of a 'stop signal' (detection), the stochastic accumulation of information (selection), and suppression of the motoric output (implementation). Furthermore, these core processes can be modulated by a set of processes that take place on shorter (seconds, minutes, hours or days) and longer (months or years) timescales. Depending on the species, this can involve, e.g., outcome monitoring, anticipatory adjustments, and both short-term and long-term learning. Here we argue that some of these cognitive processes play a role in RI across species (without assuming a one-to-one mapping for the full processing chain). In particular, in the present study we propose that one of these core processes, namely stop-signal detection, is a crucial (but largely ignored) building block of RI across species, including avian species.

The Crucial Role of Stop-Signal Detection

Several lines of evidence indicate that signal detection may play a critical role in the stopping of actions (at least in humans). For example, several behavioural studies reveal that RI is impaired when visual distractors occur in the environment (Verbruggen, Stevens, et al., 2014), or when stop signals are hard to perceive (Van Der Schoot et al., 2005). Neurophysiological and computational work also demonstrated that early perceptual processing of potential stop signals (which could be e.g., an obstacle, or in case of humans, a red light) determines to a large extent whether individuals can successfully inhibit a response or not (Bekker et al., 2005; Boehler et al., 2009; Elchlepp and Verbruggen, 2017; Pani et al., 2018; Salinas and Stanford, 2013).

Thus, it appears that RI may largely depend on the outcome of perceptual processes. However, the crucial contribution of these processes to successful RI is rarely acknowledged or studied in the non-human animal cognition domain, with a few notable exceptions. For example, researchers found that avian RI was improved when the visibility of a stop signal (i.e., a predator) was improved (e.g., when the predator occurred against a white background, in bright light, or in short grass) (Devereux et al., 2006; Nebel et al., 2019). Other studies suggested that RI in the detour barrier task is affected by the perceptual characteristics of the barrier (i.e., the type of stop signal). For example, Regolin and colleagues (Exp 1) (1994) exposed 2-day old white leghorn chickens (*Gallus gallus domesticus*) to a variety of barrier types. These included a barrier with vertical bars or stripes, and a barrier with horizontal bars. The authors found that RI performance **was impaired (i.e., the time required to successfully detour around the barrier)** when faced with vertical- than horizontal-bar barriers. Both vertical- and horizontal-bar barriers occluded the reward behind the barrier to a similar degree (i.e., 20% compared with a fully transparent barrier). Thus, the differences between these two barrier types cannot be attributed to differences in physical reward occlusion. Instead, the authors suggested two alternative potential explanations for this asymmetrical effect, namely (1) the degree of subjective occlusion and (2) the ecological validity of stop signals.

First, despite equal reward occlusion by each barrier type, the behavioural repertoire of ground-moving animals consists primarily of horizontal movements (e.g., walking, running). Consequentially, these animals can 'subjectively' perceive a reward as less occlusive (i.e., more visible) with vertical- than horizontal-bar barriers (making it harder to inhibit the response to go directly for the reward) (Kabadayi, Bobrowicz, et al., 2018). However, follow-up experiments in which the occlusion of the reward was directly manipulated, were inconsistent with this 'subjective occlusion' account (Regolin, Vallortigara, et al., 1994). Second, differential performance between vertical- and horizontal-bar barriers might be due to the ecological niche of the species. Gallinaceous birds such as chickens are mainly terrestrial animals that have occupied niches that consist of penetrable long grass and twigs. Regolin et al. (1994) therefore argued that it might be harder for gallinaceous birds to detour around vertical- than horizontal-bar barriers, as the former would mimic the penetrable vertical vegetation of their ecological niche (whereas in the detour task, the vertical-bar barrier is of course, not penetrable).

Zucca and colleagues (2005) further investigated this ecological-niche hypothesis by comparing detour performance in another gallinaceous bird species, hybrid (Japanese) quails (*Coturnix coturnix x C. japonica*), and two species with a substantially different ecological niche, namely yellow-legged gulls (*Larus michahellis*)¹ and domestic canaries (*Serinus canaria*). They used a variant of the detour task with multiple compartments and again, vertical- and horizontal-bar barriers (14% reward occlusion compared with a transparent barrier²). In this study, the authors considered both probability of a correct response (i.e., going to the correct compart-

¹Zucca and colleagues (2005) mention in their paper that they tested herring gulls, but used the scientific name of the Caspian gull *Larus cachinnans*. The taxonomy of the genus *Larus* has been updated over the years. Given that the authors mentioned that the gulls were from a breeding colony in Trieste (Italy), we assume they tested yellow-legged gulls, which were formerly treated as a subspecies of the herring gull (as was the Caspian gull).

²Zucca and colleagues (2005) mention that they used a 23 x 26 cm barrier, barrier lines/rods with a width of 0.2 cm, and in-between line/rod gaps of 1.25 cm. Given these measurements, only a combination of 18 rods/lines and 18 in-between gaps is possible, which is the equivalent of a vertical- or horizontal-bar barrier with a 14% reward occlusion

101 ment during their first attempt) and the latency to detour as measures of RI. They found that the detour
102 accuracy for quails was lower (i.e., RI performance was impaired) for vertical- than for horizontal-bar barriers.
103 This seems consistent with the findings of Regolin and colleagues (1994), although it should be noted that
104 Zucca et al. (2005) only found a significant effect for detour accuracy but not for the latency to detour, the
105 measure of RI in the study of Regolin et al. (1994). For yellow-legged gulls, detour accuracy was not influenced
106 by barrier type, but detour latency was. Specifically, the latency to detour was longer (i.e., RI was impaired) for
107 horizontal- than vertical-bar barriers. Again, the authors attributed this to the species' ecological niche. Specif-
108 ically, Zucca et al. (2005) argued that in the (original) ecological niche of young, yellow-legged gulls, chicks are
109 accustomed to consider the vertical ground vegetation of sand dunes as largely impenetrable. According to
110 the authors, it might therefore be harder for (young) gulls to detour around horizontal- than vertical barriers,
111 as the latter would be perceived as less penetrable (note that Zucca et al. (2005) tested juvenile gulls that
112 could not fly yet). Lastly, canaries were unable to detour around the barrier, although they made several
113 attempts to fly over the barrier demonstrating that they were sufficiently motivated. Zucca et al. (2005) there-
114 fore hypothesized that the detour task is not considered to be a real problem for the two-month old canaries.
115 The authors suggested that after all canaries are aerial birds, allowing them to tackle obstacle problems by
116 simply flying over them (but which was not possible in the detour task due to the dimensions of the used
117 apparatuses).

118
119 In sum, the results of Regolin et al. (1994) and Zucca et al. (2005) indicate that the characteristics of the 'stop
120 signal' matter in the detour task, potentially shedding new light on RI in avian species. However, some con-
121 cerns can be raised about certain features of the previous studies (which are summarized in Table 1). First,
122 the sample size was low (at least for some species), the studies (inconsistently) used within- and between-
123 species designs, the number of trials per barrier type differed within and between species and the number
124 of sessions per barrier type fluctuated between species (e.g., yellow-legged gulls received three sessions per
125 barrier type spread over three days, while hybrid quails received one session per barrier type). The latter
126 two issues are also problematic from a conceptual point of view, as previous work indicates that learning
127 will influence RI (Verbruggen, Best, et al., 2014; Verbruggen and Logan, 2008a), including in the detour task
128 (Van Horik, Beardsworth, Laker, Whiteside, et al., 2020). Second, both studies used less-common variants of
129 the detour task, which complicates comparisons with the wider literature. Additionally, they used less com-
130 mon, hard to standardize (social) rewards, which complicates between-species comparisons of RI behaviour.
131 Similarly, the large differences in developmental trajectories and the lack of adapting the test apparatus to
132 the morphological differences between species, also complicated the between-species comparisons.

133 **A Partial Replication of Regolin et al. (1994) and Zucca et al. (2005)**

134 To prove the significance of the previous study, our study will investigate the role of stop-signal detection
135 in avian RI by partially replicating the studies of Regolin et al. (1994) and Zucca et al. (2005). The importance
136 of the original studies is indubitable, as they are one of the few studies that aimed to 'deconstruct' avian RI
137 performance by focusing on the underlying cognitive processes (in this case, stop-signal detection). Addition-
138 ally, Zucca et al. (2005) implemented a comparative approach to investigate whether differences in how the
139 stop signal might be perceived by different species could contribute to variation in stopping behaviour.

140
141 In our partial replication, we will make several changes to address commonly raised concerns in the detour
142 literature (including the concerns raised in the previous section, see table 1). First, we will directly compare
143 four species (white leghorn chickens, Japanese quails, herring gulls (*Larus argentatus*³) and domestic canaries),
144 in a well-powered mixed design analysis with *Species* as between-species factor, and *Barrier* (vertical-bar vs.
145 horizontal-bar barrier) as within-species factor. All species will be given an equal amount of trials and ses-

³Given the high availability of the herring gull at the North Sea coast (Belgium), herring gulls were selected to represent the gull species in this comparative study. But see also footnote 1.

Table 1. Methodological features of the Regolin et al. (1994), the Zucca et al. (2005) and the present study.

Source	Regolin (1994)	Zucca (2005)			Current Study
1. Methodology					
Species	White leghorn chicken	Hybrid quail	Yellow-legged gull	Canary	All four species
Design	Between	Between	Within	Within	Mixed
Total Sample	750 (250) ¹	90	5	26	240 (60/species)
Sample per Barrier Type	102 (34) ¹	18	5	26	60/species
Trials per Barrier Type	1	10	10	1 or 10 ²	3
Sessions per Barrier Type	1	1	3	1	1
2. Detour Task	Two compart.	Four compart.	Four compart.	Four compart.	Simple
3. Reward	Cagemates	Reflection	Reflection	Reflection	Food
4. Baseline covariate	No	No	No	No	Yes
5. DV's	Latency	Latency Accuracy	Latency Accuracy	Latency Accuracy	Latency Persistence
6. Enclosure					
Social density	3	1	5	5	10
Fence	NA	Vertical	Bricks	Vertical	Mesh netting
7. Test Age	2 days	1 M	10-25 days	4-6 M	Species specific
8. Apparatus					
Test box: L x W	120 x 35	150 x 75	150 x 75	150 x 75	Scaled/species
Test box: H	60	40	40	40	Barrier H
Barrier-Entry Distance	27	27	27	27	Scaled/species
Barrier: L x H	10 x 20	23 x 26	23 x 26	23 x 26	Scaled/species
Barrier line: W	0.3	0.2	0.2	0.2	Scaled/species
Gap between barrier lines	1.2	1.25	1.25	1.25	Scaled/species

Note. DV's = Dependent variables, ¹ = Animals were reared and tested in groups of three. The means of each trio was used as individual data for the subsequent analysis; ² = 6/26 canaries received 1 trial/barrier, 20/26 canaries received 10 trials/barrier. Measurements are in cm.

146 sions per barrier type (see below). Second, the perceptual characteristics of the barrier (i.e., vertical-bar vs.
147 horizontal-bar barriers) will be manipulated in a simple detour barrier task (which is the most common vari-
148 ant of the detour problem; (Kabadayi, Bobrowicz, et al., 2018), rather than a four- (Zucca, Antonelli, et al.,
149 2005) or two-compartment (Regolin, Vallortigara, et al., 1994) detour task). See figure 1, for an overview of
150 the designs. Third, the unconditional reward will be food instead of a social stimulus (as in Regolin, Vallorti-
151 gara, et al., 1994 and Zucca, Antonelli, et al., 2005). Food is a common reward in laboratory tests and has a
152 high incentive value across species and individuals. Furthermore, it's subjective value can be better standard-
153 ised both within and between species compared to social rewards. Fourth, non-cognitive, motivational states
154 can influence detour performance (Kabadayi, Krasheninnikova, et al., 2017; Van Horik, Langley, et al., 2018).
155 Therefore, we will collect for each individual a 'multi-baseline' measure of their general motivational state
156 (which could be a combination of, e.g., non-transparent obstacle neophobia, test box neophobia, food moti-
157 vation, motivation to explore). This 'multi-baseline' measure will be obtained with an opaque barrier during
158 habituation (see below). We will include this as a covariate in our statistical models to increase the likelihood
159 of detecting barrier type effects within species conditional on/adjusted for the 'multi-baseline' measure of an
160 individual's general motivational state⁴. Fifth, our study will consider two measures of interest, namely the

⁴The original studies administered a variety of barrier types, including a transparent barrier, which was then also used to interpret

161 latency to detour (Regolin, Vallortigara, et al., 1994; Zucca, Antonelli, et al., 2005) and the **time spent in proxim-**
162 **ity to the barrier (persistence)**. The last variable was not included in the original studies, but adds substantial
163 information about variation in (un)successful inhibition following the different barrier types. Note that this
164 measure also captures 'accuracy', as all birds that do not peck at the barrier (i.e., an accurate response) will
165 get a score of 0, whereas all birds that do peck, will get a score > 0. Sixth, for all species, (fledged) chicks will be
166 raised in groups of 10 individuals, as variations in detour performance have already been reported with fluc-
167 tuating social group sizes (Ashton et al., 2018). Furthermore, mesh netting will be used for the enclosures of
168 all species (preventing variation in experiences with (im)penetrable vertical- or horizontal-bar objects in the
169 enclosures). Seventh, detour performance of the different species will be compared when they are on similar
170 levels in their developmental trajectory (see e.g., Kabadayi, Jacobs, et al. (2017), Kabadayi, Krasheninnikova,
171 et al. (2017) and Verbruggen, McLaren, et al. (2014) for the influence of cognitive maturation on RI), and again,
172 with similar experiences in the enclosure, keeping in mind the precocial-altricial spectrum (see below). Finally,
173 the size of the test apparatuses and barriers (including the width and the in-between line gaps) will be scaled
174 based on the morphological characteristics of each species (see below). For example, Zucca et al. (2005) used
175 the same test box for all three species, and argued that this was appropriate because they tested species at
176 different ages. Nevertheless, one could still expect substantial differences in body size (e.g., a one-month old
177 Japanese quail is substantially larger than a two-month old canary). As (relative) distance towards the reward
178 influences detour performance (Kabadayi, Bobrowicz, et al., 2018), it is therefore important to control for this
179 as well.

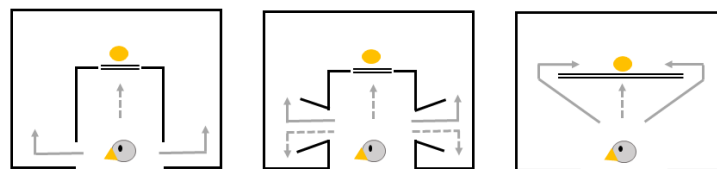


Figure 1. A display of the three detour task variants: the two-compartment detour task (left, Regolin, Vallortigara, et al., 1994) the four-compartment detour task (middle, Zucca, Antonelli, et al., 2005) and the simple detour barrier task (right, current study). Double line: barrier; **full arrows: correct responses; dashed arrows: incorrect responses.**

Predictions

180
181 First, we predict better RI performance for ecologically valid compared with non-valid stop signals, as
182 should be reflected in shorter latencies to detour and less time spent persisting. As the (original) ecological
183 niche of our species substantially differs (white leghorn chicken and Japanese quails: penetrable vertical ter-
184 restrial vegetation; herring gulls: impenetrable vertical vegetation of sand dunes; domestic canaries: aerial en-
185 vironment), the ecological validity of stop signals will be species-specific. Specifically, for white leghorn chick-
186 ens and Japanese quails, we expect better detour performance for horizontal- (HB) compared with vertical-bar
187 barriers (VB; thus, detour performance HB > VB). We expect the opposite pattern for herring gulls (i.e., detour
188 performance HB < VB). Finally, based on the findings of Zucca et al. (2005), we do not expect differences
189 between vertical- and horizontal-bar barriers for canaries (i.e., detour performance HB = VB). Overall, this
190 pattern should thus result in a statistical interaction between *Barrier* and *Species* (**Prediction 1**).

191
performance with the other barrier types. Yet, we opted to exclude transparent barriers from our design for **three reasons**. First, the comparison of transparent and barred barriers tests another hypothesis, namely the role of reward occlusion, rather than the ecological validity of the barrier type (which can only be tested by comparing vertical- and horizontal-bar barriers). **Second, performance in the detour task can be influenced by differential individual experiences with transparent obstacles** (Kabadayi, Krasheninnikova, et al., 2017; Van Horik, Langley, et al., 2018). Last, omitting the transparent barrier reduces the contact of wild herring gulls to humans, which is important as herring gulls are wild animals and will be raised as such, prior to their post-test release back to nature.

192 Second, as each session will consist of three trials (of the same barrier type), we can also look at how detour
193 performance improves within each session. Based on previous studies, we predict that detour performance
194 will improve across trials within a session (**Prediction 2**).

195

196 Furthermore, we will *explore* if the learning effect (i.e., improved detour performance across trials) interacts
197 with the ecological validity of the stop signals. **There are two possible patterns that would result in a three-way**
198 **interaction between *Species*, *Barrier* (horizontal- vs. vertical-bar barriers), and *Trial* (1-3) (**Explorative Predic-****
199 **tion 3)**. First, detour performance might be better for ecologically valid compared with non-valid stop signals
200 at the beginning, but this pattern might diminish over time as individuals learn to stop (i.e., the differences
201 between barrier types would decrease). Second, detour performance might be poor at the beginning for
202 both barrier types, but learning to stop might be easier for ecologically valid signals compared with non-valid
203 stop signals (i.e., the differences between barrier types would increase). Both patterns would be theoretically
204 meaningful, but we do not have *a-priori* predictions about the direction of the three-way interaction.

205

206

Methods

207

Subjects and Housing

208 Japanese quails, herring gulls and white leghorn chickens will be raised and tested at the avian research
209 facilities of Ghent University (Lab number LA1400452), located at the Wildlife Rescue Center (WRC) in Ostend
210 (Belgium). The canaries will be raised and tested at the avian research facilities of the University of Antwerp
211 (Lab number 1100161) in Wilrijk (Belgium).

212

Sample size

213 We will test 60 individuals per species. *A-priori power sensitivity analyses done in G*Power (Faul et al.,*
214 *2009) indicate that this is sufficient to detect small effects; it is also the largest number that is practically*
215 *feasible⁵*). *For the sensitivity analysis, we used a mixed ANOVA model with one between-subjects factor (4*
216 *levels; corresponding to our *Species* factor) and two within-subjects factor (one with 2 levels – *Barrier* – and*
217 *one with 3 levels – *Trial*). This indicated that our sample size of 60 animals per species (240 in total) is sufficient*
218 *to detect a *Species* x *Barrier* interaction effect (**Prediction 1**) with a small effect size (Cohen's *f* effect size of*
219 *0.12; Cohen, 1988; Power = .80; cor. among RM = 0.5; we used an alpha of .025 to correct for the fact that*
220 *we will have two dependent variables measuring (slightly) different aspects of detour performance). Second,*
221 *our sample size is sufficient to detect a small effect of *Trial* (**Prediction 2**; Cohen's *f* effect size of 0.09; Cohen,*
222 *1988). Third, our sample size is sufficient to *explore* a small effect (Cohen's *f* effect size of 0.09; Cohen, 1988)*
223 *for the *Species* x *Barrier* x *Trial* interaction effect (**Explorative Prediction 3**).*

224 *Our sensitivity analyses are based on mixed ANOVAs (fixed-effects models with between- and within-species*
225 *factors). However, as discussed below, we will analyse our data with (G)LMMs, which are currently not covered*
226 *by G*Power or most other power-estimation tools. These mixed-effect models are more flexible in assigning*
227 *variance as they allow for the specification of both fixed and random effects. However, by accounting for*
228 *unexplained variance (see below), our proposed mixed effect models are more powerful than the fixed-effect*
229 *model ANOVAs used in our sensitivity analyses (and than the models used in the studies of Regolin, Vallor-*
230 *tigara, et al., 1994, and Zucca, Antonelli, et al., 2005). Thus, the sensitivity analyses discussed here are a*
231 *conservative estimate.*

⁵Farrar et al. (2020) mention in their paper on replications in comparative cognition that power analyses are not the golden standard in this research domain, and 'in many cases comparative cognition researchers could be better off performing design or sensitivity analyses based on their resource constraints.'

White leghorn chickens and Japanese Quails

Chicken and quail eggs will be obtained from local breeders in Belgium. At the WRC, the eggs will be incubated in Brinsea Ova-Easy incubators (temperature = 37.5°C; humidity = 45% for first 15 [quail] or 17 [chicken] days, after which humidity = 70% till hatching). Once hatched, chicks will receive a unique colour ring combination prior to being housed in groups of 10 chicks per indoor enclosure (size = 1m x 1m x 2m; L x W x H; ambient temperature = 15-25°C; humidity = 40% - 80%; photoperiod = 14:10 L:D; type of wire fencing = mesh netting). Birds will be *ad libitum* provided with a chicken meal mixture (Aveve Chicken Start Mash) and water. Shelter, additional heating panels (30 x 30 cm; till Day 7), and pecking objects (pine cones) will be available. The (precocial) chickens and quails will be tested at ± 3 weeks (see below for justification of species-specific test age). After testing, the individuals will be euthanized by certified staff.

Herring Gulls

Herring gull eggs will be collected by the 'Agentschap voor Natuur en Bos' and the gull patrol team in Ostend (<https://www.oostende.be/meeuwen>) who are authorized to remove gull eggs along the Belgium coast for various reasons. The eggs are collected prior to pipping, and are safely transported to the WRC. At the WRC, the eggs will be further incubated in Brinsea Ova-Easy incubators (temperature = 37.5°C; humidity = 45%) and checked twice per day for signs of pipping. When gull embryos have reached the pipping stage, they will be placed in a hatchery (temperature = 37.2°C; humidity = 50%). Once hatched, the semi-precocial gull chicks will receive a unique colour ring combination prior to being placed in boxes with netting bottoms (size = 1.20m x 0.60m x 0.60m; L x W x H) within heated rooms (ambient temperature = 15-25°C; humidity = 40% - 80%; typical photoperiod = the natural photoperiod at the latitude of Belgium; type of netting = grid) for 5 days (and till their body mass exceeds 60 grams). During this period, the gulls are hand-fed small pieces of fish and dog pellets (soaked in water), supplemented with Akwavit (Kiezebrink Focus on Food, The Netherlands). We will also provide one heating panel per box. After this initial indoor period, the gull chicks will be housed in groups of 10 individuals per outdoor enclosure (size = 5 m x 1,95 m x 2,65; L x W x H), type of wire fencing = mesh netting), with an extra heating panel for the first couple of days (note that the exact number of days will depend on the weather conditions). Food (a mixture of 75% dog food soaked in water and 25% defrosted fish, supplemented with Akwavit) will be provided four times per day (the default policy at the WRC); water will be provided *ad libitum*. The (semi-precocial) gulls will be tested when they are approximately 3 weeks old (see below). After testing, herring gulls will be moved to large flight cages to dehabituate them from human handling (and hence improve their survival rates). They will be released into the wild when they are approximately 8-10 weeks old.

Domestic canaries

Domestic canaries (of the Fife Fancy type) will be obtained from long-term, breeding populations at the Department of Biology ('Behavioural Ecology and Ecophysiology' research group) of Antwerp University. Canaries are altricial species, and nestlings are thus highly dependent of their parents for food. Therefore, chicks will only be separated from their parents at the end of the nestling period (i.e., when they are ± 25 days old) (Garcia-Co and Müller, 2022). At this point, the canaries will be moved in groups of 10 individuals to indoor aviaries of Antwerp University (size : 1m x 2m x 2m; L x W x H; ambient temperature = 15-25°C; humidity = 40% - 80%, photoperiod = the natural photoperiod at the latitude of Belgium; type of wire fencing = mesh netting). The canaries will be marked with a permanent marker for individual recognition at hatching, and ringed with a closed metal ring when their body mass exceeded the predetermined threshold of 7 g. Upon arrival at the indoor aviaries, canaries will receive a unique number-color ring combination (the default policy at the University of Antwerp). In the aviaries, canaries will be provided with canary seed mixture and egg food (van Camp, Belgium), water, shell grit, and cuttlefish bone *ad libitum*. They will be tested at 7 weeks (approximately three weeks after fledging; see below). After testing, non-native, canaries will return to their local breeding

277 population in the University of Antwerp.

278

A Comparative Testing Age

279 Our previous work (Troisi et al., 2022) indicates that 3 weeks is an ideal testing age for large gulls (incl. her-
280 ring gulls) in detour tasks and other related cognitive tests. Herring gulls are semi-precocial, but only require
281 hand-feeding for the first couple of days (and most start eating independently after two/three days). Further-
282 more, the gull chicks can already move around (and explore their environment) from Day 1. White leghorn
283 chickens and Japanese quail are precocial, which implies that they can feed independently and explore their
284 environment from Day 1. Given the overall similarities, we will therefore test white leghorn chickens, Japanese
285 quail and herring gulls when they are approximately 3 weeks old (i.e., habituation will happen \approx on day 16-18;
286 testing will happen on \approx day 19-20). By contrast, canaries only become independent when they are approxi-
287 mately 25 days old (see previous subsection). At this point they will be moved to larger enclosures and housed
288 in groups. To ensure that the altricial canaries have a similar (15-day) experience with their enclosure and their
289 cagemates as the (semi-)precocial species, habituation and testing of canaries will be delayed with 25 days
290 (i.e., habituation will happen \approx on day 41-43; testing on \approx day 44-45)

291

Apparatus

292 For each species, the test apparatus will consist of a two door start box, a test box, a barrier, and a feeding
293 bowl. Performance of the birds will be monitored using a camera placed centrally at the top of the testing
294 arena (Sony Action Cam HDR-AS50). In the test box, a vertical- or horizontal-bar barrier will block the direct
295 path to the unconditional reward (i.e., the food in the bowl) that will be immediately placed behind the barrier.
296 The species-specific unconditional food reward (white leghorn chickens and Japanese quails: chicken meal,
297 herring gull: dog pellets and fish, canaries: canary seed mixture and egg food) will consist of clearly visible
298 food, placed in a coloured bowl. To avoid satiation after the first trial on test trials (see next section), the pile
299 of food will be largely covered with a transparent perspex cover, with only a small bit of accessible food placed
300 on top of the cover. The vertical- and horizontal-bar barriers will be made of transparent perspex on which
301 18 vertical and horizontal lines, respectively, will be painted per species (see below). To prevent canaries from
302 flying over the barrier (as an alternative way of avoiding the barrier), floor-to-ceiling barriers will be used for
303 all species.

304

305 The size of the test apparatus will be adjusted per species. In a recent study from our lab, we tested herring
306 gulls in a detour task (akin to the task proposed here, but with transparent and non-transparent barriers). In
307 this study, the starting box was 35 x 20 x 26cm (L x W x H), and the test box was 145 x 88 x 132 cm (L x W x
308 H). The barrier was 40 x 40 cm (L x H), and was placed 50 cm from the start box entrance (with approximately
309 24 cm between the edges of the barrier and the sides of the test box). In the present study we will use the
310 same set-up for the herring gulls, and re-scale all values based on tarsus length at testing age (see Table 2 for
311 the values for each species). For the white leghorn chickens, Japanese quails and herring gulls we will use the
312 growth curves (figure 2) for tarsus length reported in previous studies (Dudusola and Bashiru, 2020; Troisi
313 et al., 2022; Yeasmin and Howlader, 2013). For canaries, no such growth curves were available. However, in a
314 recent study, Garcia-Co et al. (2022) measured tarsus length at day 25. Given that morphological traits (incl.
315 tarsus) seem to plateau at a similar moment in the lifespan of a canary, we will use this tarsus measure at
316 day 25 as our measure for the tarsus at testing age. In addition, the black painted barrier lines (18 in total per
317 species) will occlude the food reward by approximately 14% (Zucca, Antonelli, et al., 2005). As a consequence,
318 the width of the barrier lines (and of the in-between gaps) as described in the study Zucca and colleagues
319 (2005) will be adjusted to the re-scaled barrier size dimensions per species (see Table 2).

Table 2. The upper table shows the tarsus length and species-specific re-scaled test apparatuses based on the herring gull detour set-up of Troisi et al. (2022). The lower table shows the re-scaled width of the barrier lines (and of the in-between gaps) for each species based on the detour set-up of Zucca et al. (2005)

	White leghorn chicken	Japanese quail	Herring gull	Fife Fancy Canary
Source	Yeasmin (2013)	Dudusola (2020)	Troisi (2022)	Garcia-Co (2022)
Test age (days)	19	19	19	44
Sample size	130	2591	42	69
Mean Tarsus (mm)	30.71	25.32	55.56	17.81
Ratio	1.81	2.19	1	3.12
Apparatus (rescaled)				
Start box: L x W	19.35 x 11.05	15.95 x 9.11	35 x 20	11.22 x 6.41
Test box: L x W	80.15 x 48.64	66.08 x 40.10	145 x 88	46.48 x 28.21
Barrier-Entry Distance	27.64	22.79	50	16.03
Barrier: L x H	22.11 x 22.11	18.23 x 18.23	40 x 40	12.82 x 12.82

	White leghorn chicken	Japanese quail	Herring gull	Fife Fancy Canary
Barrier line: W	0.17	0.14	0.31	0.10
Gap between barrier lines	1.06	0.87	1.91	0.61

Note. The estimated tarsus length at testing age for (semi-)precocial species, is derived from a linear equation using the two nearest measuring points for a mixed-sex sample (except for white leghorn chickens, where an additional average was calculated over pullets and cockerels). For re-scaling the test apparatuses, the unrounded factor per species was utilized. Unless specified otherwise, measurements are in cm.

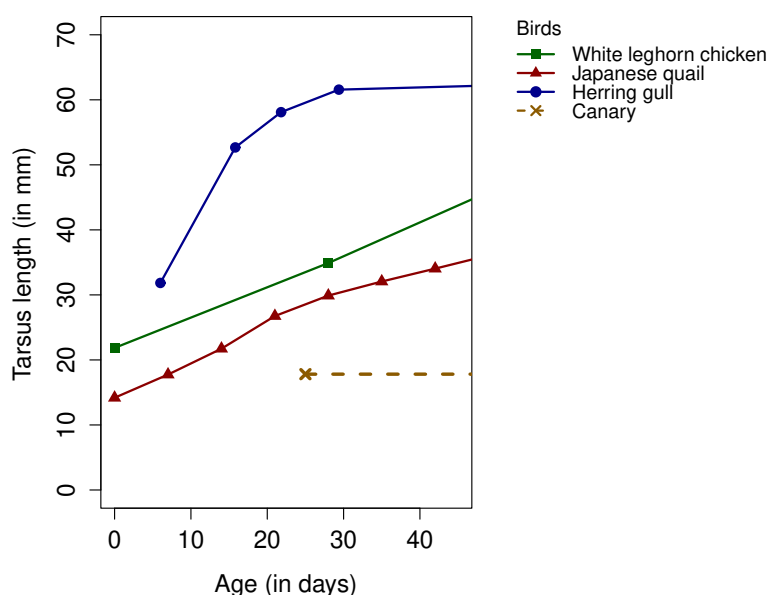


Figure 2. Full lines: reported tarsus growth during early life for white leghorn chickens (Yeasmin and Howlider, 2013), Japanese quails (Dudusola and Bashiru, 2020) and herring gulls (Troisi et al., 2022). Dashed lines: hypothetical tarsus length for canaries based the assumption that tarsus length does not change (much) after fledging (Garcia-Co and Müller, 2022)

320

Procedure

321 Prior to the start of the experiment, birds will be habituated for 10 days in their enclosure to feed from
 322 a coloured food bowl. For all species, the feeder will be placed on the ground, to simulate ground feeding
 323 during the test. When they reach the appropriate age (see above), animals will be tested for five consecutive
 324 days (i.e., three habituation and two testing days). Food is provided *ad libitum*, but in the evening before an
 325 individual's habituation or testing day, the feeders will be removed from the enclosures at 6PM (after the

326 last feeding time). This will create a non-feeding period during the night (which is normal and also happens
327 in non-experimental conditions), followed by (shortly) delayed feeding in the morning to prevent birds from
328 overindulging prior to habituation or testing. This is in line with other studies using the same species (chicken:
329 e.g., Bollweg and Sparber, 1998; quail: e.g., Ueno and Suzuki, 2014 and unpublished data from our lab; her-
330 ring gulls: e.g., Dewulf et al., 2022; domestic canaries: e.g., Müller et al., 2008). After all individuals of one
331 enclosure have completed the habituation or testing trials for the day, food will again be provided *ad libitum*.

332
333 On the three habituation days (08:00 AM - 10:30 AM), each bird will receive 1 trial per day where it can
334 freely explore the test box and feed from a centrally placed coloured food bowl. During the second and third
335 habituation day, an opaque barrier will be placed just behind the coloured food bowl. This will allow us to
336 obtain a 'multi-baseline' measure of an individual's general motivational state (which could be a combination
337 of e.g., non-transparent obstacle neophobia, test box neophobia, food motivation, motivation to explore; see
338 below). The current habituation set-up (i.e., the food bowl *in front* of the barrier) is designed in such a way
339 that acquiring a motor routine during habituation is unnecessary and cannot confound subsequent detour
340 performance with the barred barriers (Van Horik, Beardsworth, Laker, Whiteside, et al., 2020).

341 On the two testing days (10:30AM - 02:30 PM), each bird will perform one session, each consisting of 3 trials
342 with one barrier type. The order of barrier type (i.e., horizontal-bar or vertical-bar barrier) will be pseudo-
343 randomized within and between species, across the two testing days.

344
345 Due to the natural breeding season of the wild herring gull and the domestic canary, birds hatch non-
346 simultaneously. In order to guarantee an appropriate test age (see above), we will group individuals of a
347 similar age per enclosure; and then habituate or test birds per enclosure (by taking into account the aver-
348 age age of the enclosure). Although there is no fixed breeding season for Japanese quails and white leghorn
349 chickens, incubation will happen in 'batches' (due to reduced egg production/supply). As a result, an identical
350 grouping procedure within these species will be applied.

351
352 At the beginning of each trial, each bird will be gently placed in the dark two-door start box. The trial will
353 start when the researcher opens the first non-transparent cardboard door of the start box. This permits the
354 bird to see the test arena but not access it. After 15 seconds, the second, transparent door of the start box
355 will be opened and the bird can enter the test box. If the bird does not exit the start box within 30 seconds,
356 it will be gently pushed forward (by sliding the back of the starting box forward; Troisi et al., 2022). The habit-
357 uation trials will end when the individual eats from the food bowl for 30 seconds or when the maximum trial
358 time has been reached (i.e., 5 min 15 seconds). The test trials will end immediately when the individual eats
359 from the food bowl (to avoid food satiation on subsequent trials) or when the maximum trial time has been
360 reached (i.e., 2 min 15 seconds). Maximum trial times during habituation will be longer than during testing, as
361 the main goal of the habituation is to familiarize each bird with the test material (and obtain a 'multi-baseline'
362 measure of an individual's general motivational state). The maximum duration of a test trial will be 2 minutes
363 (after an additional 15 seconds inside the start box with the second, transparent door), which is in line with
364 other studies (e.g., Kabadayi, Krasheninnikova, et al. 2017 and Vernouillet et al. 2016). Two minutes should be
365 sufficient, especially because our barriers are not entirely transparent (hence, will partially occlude the food
366 reward), making it easier to execute a detour response (Kabadayi, Bobrowicz, et al., 2018).

367
368 We plan to test herring gulls during the second half of June 2023 (restricted to breeding season), Japanese
369 quails in Autumn 2023, white leghorn chickens in late Winter 2024, and canaries in late spring 2024 (again,
370 restricted to breeding season).

Data Processing and Analysis

Video Recording and Analysis

The videos of the second and third habituation trial and the three test trials per test session will be coded using the free, open-source 'Behavioural Observation Research Interactive' Software (BORIS, v.7.13.6) (Friard and Gamba, 2016). We will code five (types of) events (see table 3 and figure 3): latency to leave the start box (for the 2 habituation trials and the six test trials), persisting (test trials only), moment of detouring the barrier (test trials only), interacting with the food bowl (for the 2 habituation trials and the six test trials) and leaving the species-specific 'test box zone of interest' (test trials only). All videos will be coded by the first author. A second person, blind to the hypotheses will code 10% of the videos per species. An average Cohen's Kappa (McHugh, 2012) will be calculated for these videos to provide a measure of inter-rater, cross-species reliability. In the case that no perfect inter-rater, cross species agreement ($0.81 \leq \text{Cohen's Kappa} \leq 1$) has been reached, discrepancies in inter-rater reliability will be investigated by calculating the average Cohen's kappa (McHugh, 2012) for each species, separately. By doing so, a species-specific or overall low Cohen's Kappa will reveal whether the videos have to be recoded for one or all four species.

To compare detour performance between species, we will extract our two response variables from the behavioural events coded in BORIS. First, the latency to detour (in seconds) will be determined as the time between leaving the start box and the moment the individuals detours the barrier. Second, the time spent persisting (in seconds) will be calculated as the cumulative time that the individual spends in the species-specific 'barrier zone of interest' (size = Barrier L x 25% of the Barrier-Entry Distance; L x W, see table 2 for the species-specific dimensions). Third, a 'multi-baseline' measure of an individual's general motivational state (in seconds) will be calculated, by averaging the time between leaving the start box and touching the food (bowl) placed in front of the opaque barrier on habituation trial 2 and 3. Note that if a bird is unsuccessful on trial 2, a non-averaged 'multi-baseline' score will be calculated based on habituation trial 3 only.

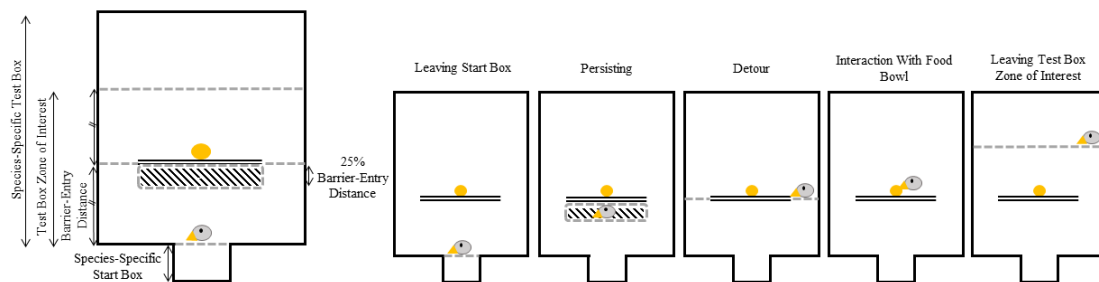


Figure 3. Visualisation of the species-specific dimensions (left) and the behaviours (right) that will be coded in BORIS. Double line: Barrier; hatched area: species-specific 'barrier zone of interest'; dashed lines: (fictitious) lines that need to be crossed by the bird, see table 3.

Data Exclusion Criteria

Individuals that fail to visit the food bowl at the third habituation day, will be excluded from subsequent test trials (pre-test criterion). This exclusion criterion guarantees a similar within- and between-species proficiency with the basic task demands (e.g., the perceptual, motoric and motivational requirements to retrieve a food reward; for a similar pre-test exclusion criterion see, MacLean et al., 2014).

Birds that did not detour around the barrier nor entered the species-specific 'barrier zone of interest' in a test trial, will be excluded from subsequent test trials (and data of that individual will be excluded from all

Table 3. The description of the behaviours that will be coded in BORIS.

Behaviour	Description
Leaving start box	- When the bird voluntarily leaves the start box: when both feet of the bird are visibly inside the test box, or (when the feet are not visible) when the front body half of the bird is inside the test box. - When the bird needs to be pushed: When the bird's entire body is inside the test box ¹ .
Persisting	At least the bird's whole head crosses the (fictitious) lines of the rectangular-shaped, species-specific 'barrier zone of interest' ² .
Detour	At least the bird's whole head crosses the (fictitious) straight line from the barrier to the side of the test box (with a modifier whether they detour on the right or left side)
Interaction with food bowl	Bird touches the food or food bowl with its beak.
Leaving the 'test box zone of interest'	At least the bird's whole head crosses the (fictitious) straight line at $\approx 2/3$ of the test box length ² .

Note. ¹ = When a bird needs to be gently pushed, it is most likely that the individual was lying down in the start box. As a result, a gentle push will put the bird forward and will result in the bird ending up in a standing position in the test box. As a result, we will code whether these individuals have left the start box when the bird's entire body (vs. front half body) is inside the test box. ² = The fictitious lines that mark a zone of interest are defined by two wooden sticks attached to each side of the test box.

403 statistical analyses). This mid-test exclusion criterion will be applied for two reasons. First, birds that do not
404 obtain a measure for one of the two dependent variables within 2 minutes are likely to be unmotivated or
405 be in distress. Furthermore, observations from similar RI test paradigms in our lab demonstrate that such
406 individuals are unlikely to eat at all with a prolonged test time or on subsequent test trials (within the same
407 day).⁶ In addition, removing birds from subsequent trials (rather than assigning a maximum trial limit for
408 both dependent variables) reduces the risk of data skewing.

409 Individuals that have left the species-specific 'test box zone of interest' (size = 2 times the Barrier-Entry
410 Distance, see table 2 for the species-specific dimensions) without touching the food (bowl) will also be ex-
411 cluded from further testing and all analyses. This mid-test exclusion criterion assures that we avoid confus-
412 ing general exploration behaviour (without initial interest in the food) with successful detour performance
413 (which assumes interest in the food). Thus, by excluding birds with differential trial experiences (due to e.g.,
414 demotivation, distress, distraction or exploration; for a similar mid-test exclusion criterion see, Van Horik,
415 Beardsworth, Laker, Langley, et al., 2019), we aim to ensure that each barrier orientation is standardized
416 within- and between species.

417 Note that we expect that we can maintain our sample size by replacing all excluded birds, because we
418 generally incubate 20% more eggs than the number of individuals required for the testing (to account for
419 possible drop outs during the whole study).

420

Statistical Analysis

421 Statistical analyses will be performed using R. v. 4.2.2 (R Core Team, 2021). Models will be fitted by means
422 of the *lme4* package (Bates et al., 2015) and parameter estimation and p-values for the generated models
423 will be provided by means of the *lmerTest* package (Kuznetsova et al., 2017) via the Satterthwaite's degrees of

⁶In a continuous RI task with a sample size of 80 herring gulls, birds that failed on the first trial, were likely to fail again on the second trial of the same test day (Dewulf et al., 2022).

424 freedom method (linear mixed model, LMM) or via the *carData* (Fox, Weisberg, and Price, 2022) and *car* (Fox
425 and Weisberg, 2019) packages (generalized linear mixed model, GLMM). For the (G)LMM, we will use partial
426 eta-squared (η_p^2) as effect sizes and they will be calculated by means of the *effectsize* (Ben-Shachar et al., 2020)
427 package.

428

429 A (G)LMM with Type III sum of squares will be performed on the latency to detour and the cumulative time
430 spent in the species-specific 'barrier zone of interest' (persisting). Both models will include the between-
431 species factor: *Species* (i.e., white leghorn chickens, Japanese quails, herring gulls and canaries) and both
432 within-species factors: *Barrier* (i.e., vertical- and horizontal-bar) and *Trial* (i.e., 1-3), and their interactions. In
433 addition, we will add two extra explanatory variables to the model: a '*multi-baseline*' measure of an individ-
434 ual's general motivational state (and its interaction with *Species*, as we will mean-center this '*multi-baseline*'
435 measure within *Species*, see Chen et al., 2014 for an example of within-group centering); and *Barrier Order*
436 (with two levels: did the individual receive the horizontal-bar barrier on the first test day 1 and the vertical-bar
437 barrier on the second test day; or vice versa), as species might demonstrate superior performance with the
438 last encountered barrier, irrespective of its type and ecological validity. Individual birds and enclosure (social
439 group) will be included as a random intercept in the models, with individual birds nested in enclosures. In
440 addition, we will include by-individual (nested in enclosures) random slopes that can vary for the levels of
441 *Species* (corresponding with species-specific intercepts).

442 Model plots will be generated by means of the package *performance* (Lüdtke et al., 2021) to inspect for
443 violations of the model assumptions: 1) heteroscedasticity (plotting the square root of the residuals (y-axis)
444 and fitted values (x-axis)), 2) non-normality of residuals (plotting the sample quantiles (y-axis) on the standard
445 normal distribution quantiles) and 3) outliers (plotting standard residuals (y-axis) and leverage). Additionally,
446 the multicollinearity between fixed main factors (via the variance inflation factor, VIF) and the autocorrelation
447 between residuals (via a Durbin-Watson-Test) will be calculated via functions provided by the *performance*
448 package (Lüdtke et al., 2021). Potential violations of model assumptions will be addressed by transforming
449 the (in)dependent variables (i.e., via log-transformation) or by changing the error distribution (family) or the
450 link function of the model (switching a default LMM that will be fitted to a GLMM). Fixed main effects with a
451 VIF of >5 will be removed and logical outliers (i.e., recording/entry errors) will be inspected and corrected (if
452 possible). In the case that the outlier cannot be corrected, all data of that individual will be excluded from all
453 statistical analyses.

454

455 In case we find (a) significant *Barrier* x *Species* interaction effect(s) (**Prediction 1**) and/or a main effect of
456 *Trial* (**Prediction 2**), further post-hoc Bonferroni-Holm corrected (Holm, 1979) linear contrasts upon the model
457 will be performed to compare respectively, the performance with different ecological (non-)valid barriers per
458 species and performance over trials (within one session). In case we find (a) significant three-way *Species* x
459 *Barrier* x *Trial* interaction effect(s) (**Explorative Prediction 3**), further exploratory Bonferroni-Holm corrected
460 (Holm, 1979) linear contrasts upon the model will be performed to compare trial performance of species on
461 different types of the barrier. Follow-up linear contrasts and Cohen's *d* effect sizes will be calculated by means
462 of the *emmeans* (Lenth, 2023) package.

463

464

Discussion

465

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469

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475 of Sciences, Flemish Institute for Biotechnology (VIB) of Ghent University (EC2022-091).

476

Conflict of interest disclosure

477 The authors declare that they comply with the PCI rule of having no financial conflicts of interest in relation
478 to the content of the article.

479

Data, script, code, and supplementary information availability

480 Data are available online: DOI of the webpage hosting the data <https://doi.org/10.24072/fake1> Script and
481 codes are available online: DOI of the webpage hosting the script and codes <https://doi.org/10.24072/fake2>
482 Supplementary information is available online: DOI of the webpage hosting the script and codes [https://doi.](https://doi.org/10.24072/fake3)
483 [org/10.24072/fake3](https://doi.org/10.24072/fake3) The DOI hyperlinks should be active. they should also be present in the reference list and
484 cited in the text.

Question	Hypothesis	Sampling plan	Analysis Plan	Rationale for deciding the sensitivity of the test for confirming or disconfirming the hypothesis	Interpretation given different outcomes	Theory that could be shown wrong by the outcomes
<p>1 Does detour performance improve when the perceptual characteristics of the barrier (in a detour task) match the ecological niche of a bird species?</p>	<p>As we will test four bird species with substantially different ecological niches, the perception of a match between the perceptual characteristics and the ecological niche will be species-specific (see below). We therefore predict an interaction between barrier type and species.</p> <p style="text-align: center;">1:1</p> <p>For white leghorn chickens (<i>Gallus gallus domesticus</i>) and Japanese quails (<i>Coturnix japonica</i>): better detour performance for horizontal- (HB) compared with vertical-bar barriers (VB; thus, detour performance HB > VB).</p> <p style="text-align: center;">1:2</p> <p>For herring gulls (<i>Larus argentatus</i>): better detour performance for vertical-</p>	<p>We will test 60 individuals per species (total N = 240). <i>A-priori</i> power sensitivity analyses done in G*Power (Faul et al., 2009) indicate that this is sufficient to detect small effects; it is also the largest number that is practically feasible given our resource constraints and study design (see Farrar et al., (2020)) For the sensitivity analysis, we used a mixed ANOVA model with one between-subjects factor (4 levels; corresponding to our <i>Species</i> factor) and two within-subjects factor (one with 2 levels – <i>Barrier</i> – and one with 3 levels – <i>Trial</i>).</p> <p>This indicated that our sample size of 60 animals per species (240 in total) is sufficient to detect a <i>Species x Barrier</i> interaction effect (Question 1) with a small effect size (Cohen’s <i>f</i> effect size of 0.12; Cohen, 1988; Power = .80; cor. among RM = 0.5; we used an alpha of .025 to correct for the fact that we will have two dependent variables measuring (slightly) different aspects of detour</p>	<p>A (G)LMM with type III sum of squares will be used to analyse our two dependent variables, namely 1) the latency to detour and the 2) cumulative time spent in the species-specific ‘barrier zone of interest’(persisting).</p> <p>Both models will include the between-species factor: <i>Species</i> (i.e., 4 levels) and both within-species factors: <i>Barrier</i> (i.e., 2 levels) and <i>Trial</i> (i.e., 3 levels), and the two control variables (as covariates), namely (a) a ‘muti-baseline’ measure of an individual’s motivational state (and its interaction with <i>Species</i>, as we will mean-center this ‘multi-baseline’ measure within <i>Species</i>), and (b) <i>Barrier Order</i> (i.e., 2 levels). Individual birds and enclosure (social group) will be included as random effects in the models, with individual</p>	<p>We performed a-priori power sensitivity analyses (alpha corrected = .025, Power = .80, cor. among RM = 0.5) with G*Power (Faul et al., 2009) for the different effects of interest and confirmed that our sample size is sufficient to detect small effects (with a Cohen’s <i>f</i> effect size varying between 0.09 -0.12 ; Cohen, 1988).</p> <p>See sampling plan for more information.</p>	<p>This study is a partial replication of the study of Regolin et al., (1994) and the comparative study of Zucca et al., (2005). Across research fields, there is a clear need for these replication studies (see Farrar et al., 2020, for the comparative cognition field), as they are "a central part of the iterative maturing cycle of description, prediction, and explanation", and as such, play an "important, exciting, and generative role in scientific progress" (Nosek & Errington, 2020).</p> <p>As a consequence, the absence of a Barrier x Species interaction effect (which we predict on the basis of the previous studies) informs us about the</p>	<p>We propose that stop-signal detection (hence, barrier detection) is a crucial, cognitive building block of RI across species (Verbruggen et al., 2014), including birds.</p> <p>Here we will take this idea one step further and propose that ecologically valid signals are easier to detect (or to perceive as a stop signal), and this will enhance stopping.</p> <p>The role of stop-signal detection in avian response inhibition, and in particular, the interaction with the ecological niche of the species, should be revised if we cannot replicate the previous work (Regolin et al., 1994; Zucca et al., 2005).</p>

	<p>horizontal-bar barriers (thus, detour performance $HB < VB$).</p> <p style="text-align: center;">1:3</p> <p>For domestic canaries we do not expect differences between vertical- and horizontal-bar barriers (i.e., detour performance $HB = VB$)</p>	<p>performance).</p> <p>Second, our sample size is sufficient to detect a small effect of <i>Trial</i> (Question 2; Cohen's f effect size of 0.09; Cohen, 1988).</p> <p>Third, our sample size is sufficient to explore a small effect (Cohen's f effect size of 0.09; Cohen, 1988) for the <i>Species x Barrier x Trial</i> interaction effect (Question 3: Explorative).</p> <p><u>Remark 1</u>: Our sensitivity analyses are based on mixed ANOVAs (fixed-effects models with between- and within-species factors). However, as discussed below, we will analyse our data with (G)LMMs, which are currently not covered by G*Power or most other power-estimation tools. These mixed-effect models are more flexible in assigning variance as they allow for the specification of both fixed and random effects. However, by accounting for unexplained variance (see below), our proposed mixed effect models are more powerful than the fixed-effect model ANOVAs used in our sensitivity analyses (and than the models used in the studies of Regolin,</p>	<p>birds nested in enclosures. In addition, we will include by-individual (nested in enclosures) random slopes that can vary for the levels of <i>Species</i> (corresponding with species-specific intercepts).</p> <p>Model plots will be generated by means of the package <i>performance</i> (Lüdecke et al., 2021) to inspect for violations of the model assumptions: 1) heteroscedasticity (plotting the square root of the residuals (y-axis) and fitted values (x-axis)), 2) non-normality of residuals (plotting the sample quantiles (y-axis) on the standard normal distribution quantiles), and 3) outliers (plotting standard residuals (y-axis) and leverage). Additionally, the multicollinearity between fixed main factors (via the variance inflation factor, VIF) and the autocorrelation between residuals (via a Durbin-Watson-Test) will be calculated via functions provided by the <i>performance</i> package (Lüdecke et al., 2021).</p>		<p>validity of the original findings (Regolin et al., 1994; Zucca et al., 2005) and can further emphasize on the need of replication in general.</p>	<p>486</p>
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		<p>Vallortigara, et al., 1994, and Zucca, Antonelli, et al., 2005). Thus, the sensitivity analyses discussed here are a conservative estimate.</p> <p><u>Remark 2:</u> We will incubate 20% more eggs than the number of individuals required for testing (to account for possible drop outs and guarantee statistical power during the whole study)</p>	<p>Potential violations of model assumptions will be addressed by transforming the (in)dependent variables (i.e., via log-transformation) or by changing the error distribution (family) or the link function of the model (switching a default LMM that will be fitted to a GLMM). Fixed main effects with a VIF of >5 will be removed and logical outliers (i.e., recording/entry errors) will be inspected and corrected (if possible). In the case that the outlier cannot be corrected, all data of that individual will be excluded from all statistical analyses.</p> <p>In case we find (a) significant <i>Barrier x Species</i> interaction - effect(s) (Question 1) further post-hoc Bonferroni-Holm corrected linear contrasts upon the model will be performed to compare performance with different (ecological valid) barriers per species (1:1, 1:2, 1:3).</p>			487
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Study Design Template

<p>2</p> <p>Does detour performance improve over trials?</p>	<p>2:1</p> <p>Detour performance will gradually improve over trials (thus, detour performance trial 1 < trial 2 < trial 3).</p>		<p>In case we find (a) significant main effect of <i>Trial</i> (Question 2) further post-hoc Bonferroni-Holm corrected linear contrasts upon the model will be performed to compare performance over trials (2:1).</p>		<p>The absence of a main effect of trial would demonstrate that detour performance is consistent over trials.</p>	<p>We propose that detour performance improves over trials. Extensive work on skill acquisition in humans has shown that performance generally improves rapidly at first and then more slowly over time (see e.g., Logan, 1988, Thorndike, 1913). If we do not find a difference between trials, this would indicate that detouring cannot be learned easily by avian species.</p>
<p>3 (explorative)</p> <p>Does the learning effect (i.e., improved detour performance across trials) depend on the ecological validity of the barrier?</p>	<p>3:1 (explorative)</p> <p>We will <i>explore</i> if the learning effect (i.e., improved detour performance across trials) interacts with the ecological validity of the stop signals. There are two possible patterns that would result in a three-way interaction between <i>Species</i>, <i>Barrier</i> (horizontal- vs. vertical-bar barriers), and <i>Trial</i> (1-3) (Explorative Prediction 3). First, detour performance might be better for ecologically valid compared with non-</p>		<p>In case we find (a) significant three-way <i>Species x Barrier x Trial</i> interaction effect(s) (Question 3 explorative), further exploratory Bonferroni-Holm corrected linear contrasts upon the model will be performed to compare <i>Trial</i> performance of <i>Species</i> on different types of the <i>Barrier</i> (3:1 explorative).</p>		<p>Our design enables us to investigate potential interaction effects with <i>Trial</i> (e.g., the three-way <i>Species x Barrier x Trial</i> interaction effect, Question 3 explorative), with which we can further explore whether learning effects are completely absent in our design or are influenced by the (ecological validity) of the different barrier types.</p>	<p>We will <i>explore</i> if the learning effect (i.e., improved detour performance across trials) will depend on the ecological validity of signals. If we do not find such a three-way interaction effect, we can conclude (a) that superior detour performance with ecological valid than non-valid trials is independent of trial number (in case we do find a <i>Species x Barrier</i> interaction</p>

Study Design Template

	<p>valid stop signals at the beginning, but this pattern might diminish over time as individuals learn to stop (i.e., the differences between barrier types would decrease). Second, detour performance might be poor at the beginning for both barrier types, but learning to stop might be easier for ecologically valid signals compared with non-valid stop signals (i.e., the differences between barrier types would increase). Both patterns would be theoretically meaningful, but we do not have <i>a-priori</i> predictions about the direction of the three-way interaction.</p>					<p>effect) or (b) that the interaction between the stop signal and the ecological niche of the species should be revised (in case we do not find a <i>Species x Barrier</i> interaction effect).</p>

Guidance Notes

- **Question:** articulate each research question being addressed in one sentence.
- **Hypothesis:** where applicable, a prediction arising from the research question, stated in terms of specific variables rather than concepts. Where the testability of one or more hypotheses depends on the verification of auxiliary assumptions (such as positive controls, tests of intervention fidelity, manipulation checks, or any other quality checks), any tests of such assumptions should be listed as hypotheses. Stage 1 proposals that do not seek to test hypotheses can ignore or delete this column.
- **Sampling plan:** For proposals using inferential statistics, the details of the statistical sampling plan for the specific hypothesis (e.g power analysis, Bayes Factor Design Analysis, ROPE etc). For proposals that do not use inferential statistics, include a description and justification of the sample size.

Study Design Template

- **Analysis plan:** For hypothesis-driven studies, the specific test(s) that will confirm or disconfirm the hypothesis. For non-hypothesis-driven studies, the test(s) that will answer the research question.
- **Rationale for deciding the sensitivity of the test for confirming or disconfirming the hypothesis:** For hypothesis-driven studies that employ inferential statistics, an explanation of how the authors determined a relevant effect size for statistical power analysis, equivalence testing, Bayes factors, or other approach.
- **Interpretation given different outcomes:** A prospective interpretation of different potential outcomes, making clear which outcomes would confirm or disconfirm the hypothesis.
- **Theory that could be shown wrong by the outcomes:** Where the proposal is testing a theory, make clear what theory could be shown to be wrong, incomplete, or otherwise inadequate by the outcomes of the research.

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