The interplay of prior experience and motivation in great ape problem-solving (*Gorilla gorilla*, *Pan paniscus*, *Pan troglodytes* and *Pongo abelii*)

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Abstract

Many primate species have a strong disposition to approach and manipulate objects in captivity. However, few studies have investigated what primates learn during free exploration of objects in the absence of rewards, and how previous problem-solving performance influences subsequent exploration. We confronted members of each of the four non-human great ape species (*N* = 25) with the collapsible platform task that required subjects to drop a stone inside a tube to collapse a platform and release a reward. Subjects received four successive sessions with an empty apparatus (exploration driven by intrinsic motivation) followed by four with a baited apparatus (problem-solving driven by extrinsic motivation) or vice versa. Apes who first faced an empty apparatus solved the task more quickly in the baited condition than apes who started with this condition. Moreover, apes starting with the baited condition took longer to collapse the platform in the first trial than apes who started with the empty condition. This study suggests that apes exposed to an empty apparatus prior to the test gain information that is later used to solve the task in a more efficient manner. Thus, the apes learned about action-outcome contingencies during free exploration. Moreover, it indicates that the presence of food rewards distracts apes and delays problem-solving because apes' attention is mainly focused on the food.

Keywords: primates, tool use, prior experience, intrinsic motivation, exploration

Introduction

Many animal species show interest in novel objects by orienting, approaching, or manipulating them (e.g., Berlyne & Slater, 1957; Burghardt, 2006; Glickman & Sroges, 1966; Mather & Anderson, 1999; Torigoe, 1985). Several non-human primate species, in particular, display a strong disposition to manipulate objects, with great apes, capuchins and baboons showing the greatest interest and most diverse manipulations (Glickman & Sroges, 1966; Tomasello & Call, 1997; Torigoe, 1985; Welker, 1956). Exploration of objects does not necessarily yield an immediate extrinsic reward (e.g., in the form of food) but it may enhance future problem-solving performance (e.g., Gajdon, Lichtnegger, & Huber, 2014; Polizzi di Sorrentino et al., 2014; Taffoni et al., 2014) and might be an essential component of flexible tool-use (Call, 2013). In fact, learning about action-outcome contingencies during exploration may facilitate a much broader application of this knowledge compared to situations in which the knowledge was acquired while obtaining a tangible reward such as food (Call, 2013).

Several studies have suggested that high levels of exploration can lead to increased problem-solving success in non-human animals (e.g., Benson-Amram & Holekamp, 2012; Benson-Amram, Weldele, & Holekamp, 2013; Griffin, Diquelou, & Perea, 2014; Griffin & Guez, 2014; Visalberghi & Fragaszy, 1989; Visalberghi & Trinca, 1989; Webster & Lefebvre, 2001). For example, wild spotted hyenas that showed more diverse exploratory actions were more likely to open a puzzle box than less exploratory individuals (Benson-Amram and Holekamp, 2012). Similarly, wild-caught Indian mynas that manipulated a puzzle box in more diverse ways opened more food compartments than individuals that showed less diverse manipulations (Griffin et al., 2014). Exploration has been elicited in numerous studies by extrinsic motivation, e.g., food incentives (e.g., Benson-Amram & Holekamp, 2012; Benson-

Amram et al., 2013; Griffin et al., 2014). However, what individuals learn about their environment in the absence of food incentives clearly warrants further investigation.

Intrinsic motivation may stimulate exploration of novel objects and novel environments when individuals are in a relaxed state (e.g., Hughes, 1997). Knowledge gained in such situations may enhance future problem-solving performance (e.g., Birch, 1945a; Polizzi di Sorrentino et al., 2014), since this type of knowledge is less tied to a specific situation, and it might be especially useful when encountering novel problems (Call, 2013). However, few studies have investigated the relationship between exploration and problem-solving. Before delving into those studies a terminological clarification is required. Although the term problem-solving typically refers to situations in which object manipulation is driven by extrinsic motivation (e.g., food, escape), the use of the term exploration is less clear regarding its underlying motivational substrate. For the sake of clarity, in this paper we use the term problem-solving to refer to manipulation driven by extrinsic motivation and the term exploration to refer to manipulation driven by intrinsic motivation.

In a classical study, Birch (1945a) tested chimpanzees in a food raking task. While most individuals initially failed to rake in the food with a hoe, they succeeded after a phase of free exploration with sticks, suggesting that they gained knowledge about functional features of stick-like objects. Similarly, female gibbons that were exposed to a rake before the test were faster in raking in a food reward than naive gibbons (Cunningham, Anderson, & Mootnick, 2011). Gajdon et al. (2014) reported that keas that combined objects and tubes during free exploration in the absence of a food incentive later solved a baited tube puzzle by inserting an object, suggesting that exploration enhanced later problem-solving performance. Despite these suggestive results, the fact that all keas received the same presentation order of the conditions means that subjects may have also solved the task without a prior exploratory phase. Polizzi di Sorrentino et al. (2014) used a superior design by confronting capuchin monkeys with a mechatronic board at which they could perform diverse actions that resulted in predictable outcomes in one group (i.e., the same actions led to the same outcomes) and in arbitrary outcomes in the other group (i.e., the same actions led to different outcomes; see also Taffoni et al., 2014 for a similar study with human children). For example, pushing a specific button caused a specific visual (i.e., light) and auditory (i.e., tone) response for one group while it caused varying visual and auditory responses in the other group. After a phase of free exploration a box inside the apparatus that could be opened only by one specific action was baited. Capuchin monkeys who learned about action-outcome contingencies in a predictable environment retrieved the reward more often, suggesting that exploration enhanced problem-solving performance. Dunbar, McAdam, and O'Connell (2005) investigated how chimpanzees, orang-utans and human children solved a set of four puzzle boxes. One group of subjects was exposed to the boxes before the test phase while the other group received no such exposure. One attractive feature of this study is that individuals in the exposure group did not actually manipulate the boxes, they could just look at them. Nevertheless, individuals with prior exposure were faster in solving the puzzle boxes in the test phase than those without prior exposure (though there might be a confound with order of presentation, see Dunbar et al., 2005).

Although prior experience may enhance future problem-solving performance, it may also have the opposite effect in some situations (e.g., Duncker, 1945; Hanus, Mendes, Tennie, & Call, 2011; Luchins & Luchins, 1959). For instance, Hanus et al. (2011) confronted chimpanzees with the floating peanut task, which required subjects to spit water into a vertical tube to make a shelled peanut float upwards. Some chimpanzees only solved the task after they had been provided with a new water dispenser. The authors suggest that the old water dispenser may already have had the function of drinking (and spitting at conspecifics or people) and that this prior experience hindered the chimpanzees to use it in the context of the given task ("functional fixedness effect", Duncker, 1945; Hanus et al., 2011). Hrubesch, Preuschoft, and van Schaik (2009) reported that chimpanzees stuck to a less effective problem-solving technique even though a more effective one was available and clearly observable in other group members, suggesting that prior experience hindered them to adopt a more efficient problem-solving strategy. Field data support the idea that chimpanzees stay with a familiar problem-solving strategy instead of trying new and potentially more effective ones (e.g., Gruber, Muller, Reynolds, Wrangham, & Zuberbuhler, 2011; Gruber, Muller, Strimling, Wrangham, & Zuberbuehler, 2009).

Another important modulator of problem-solving performance is individuals' motivational state. Levels of extrinsic and intrinsic motivation determine the general interest in a problem. The level of extrinsic motivation depends on the satiation of the individual and the value of the food reward (i.e., quantity and quality). Individuals with a low extrinsic motivation might perform only a few attempts to solve a problem, resulting in poor performance. However, individuals with a high extrinsic motivation might narrow down their focus onto the food and disregard other important aspects of the problem, again causing a reduced performance. For example, Birch (1945b) reported that chimpanzees presented with various problem-solving tasks performed best in a state of medium extrinsic motivation compared to a low or high state of extrinsic motivation. Extrinsic motivation was induced by varying hours of food deprivation. This study suggests that chimpanzees who were insufficiently or excessively motivated to access the food, performed worse than those who were moderately motivated. A detrimental effect of high incentives was also found in humans (e.g., Glucksberg, 1964).

The level of intrinsic motivation to engage in exploration may vary across individuals (e.g., Uher, Asendorpf, & Call, 2008; Zampachova, Kaftanova, Simankova, Landova, & Frynta, 2017) and depend on features and novelty of the objects or the environment (e.g., Dubois, Gerard, & Pontes, 2005; Hughes, 1997; Welker, 1956) and plausibly, a relaxed emotional state. For example, individuals that experience fear show avoidance reactions instead of exploring an object (Hughes, 1997; Welker, 1957). Some studies have revealed an intrinsic motivation to solve problems for their own sake. For example, Menzel (1991) gave chimpanzees a choice between performing a discrimination task to gain a piece of food, or to take a freely available one. Some of the chimpanzees consistently preferred to perform the task, although they sometimes lost food when they made mistakes. Overall, those who chose to perform the task gained less food than individuals who selected the freely available option (Menzel, 1991). More recently, Clark and Smith (2013) reported that chimpanzees showed a higher interest towards objects than towards food rewards, that is, they spent more time with a maze of opaque tubes when it was filled with non-food objects than when it was filled with food rewards. Although the non-food condition was presented first and the finding might be based on a novelty effect, chimpanzees readily explored the maze without being rewarded for doing so.

Although some studies have shown that non-human primates can benefit from exploration when they subsequently face the same task in a problem-solving situation (e.g., Birch, 1945a; Polizzi di Sorrentino et al., 2014), little is known about how problem-solving may subsequently affect exploration. In other words, whereas several studies have documented that exploration enhances problem-solving, it is unclear whether problem-solving in turn enhances or reduces exploration. Additionally, it is unclear how intrinsic and extrinsic motivation impact on subjects' first and subsequent responses after repeated task presentations. To address these questions, we sought a task with a relatively complex solution, ideally involving the use of objects in some way, that afforded two versions, one driven by intrinsic motivation (empty apparatus: exploration) and another driven by extrinsic motivation (baited apparatus: problem-solving). We selected the collapsible platform task, which was originally used with corvids and that requires subjects to drop a stone inside a box to collapse a platform located inside it to release a piece of food (Bird & Emery, 2009; von Bayern, Heathcote, Rutz, & Kacelnik, 2009).

In the current study we therefore investigated the role of prior experience in problem-solving in the four non-human great ape species using the collapsible platform task, which meets our requirements about complexity and motivation, and has not been employed with non-human primates yet. Subjects were given four sessions with the baited and four with the empty condition, counterbalanced for order of presentation across subjects. Furthermore, the inclusion of repeated trials allowed us to assess whether both types of motivation were capable of sustaining subjects' responses over time to the same degree. Based on previous studies we expected that apes with prior experience in the empty condition would be faster in the baited condition than apes without prior experience. Additionally, if subjects solved the baited apparatus faster than the empty apparatus in the very first trial, this would indicate that extrinsic motivation exerted a more potent effect on their responses than intrinsic motivation. Conversely, if subjects solved the empty apparatus more quickly than the baited apparatus, this would indicate that intrinsic motivation exerted a more potent effect than extrinsic motivation. Additionally, the setup allowed us to investigate how problem-solving affects exploration, an aspect that has received little attention compared to how exploration affects problem-solving.

Methods

Subjects

Eight bonobos (*Pan paniscus*), seven chimpanzees (*Pan troglodytes*), four gorillas (*Gorilla gorilla*) and six Sumatran orang-utans (*Pongo abelii*) housed at the Wolfgang Köhler Primate Research Center (Zoo Leipzig, Leipzig, Germany) participated in this study (*N* = 25; Table S1). There were 18 females and seven males ranging from five to 48 years of age. Seven apes were nursery reared, 15 apes were mother reared and the upbringing of three apes was unknown. All subjects lived in social groups of various sizes with access to indoor and outdoor areas. Subjects were individually tested in their indoor sleeping rooms (hereafter, “test rooms”). They were neither food- nor water-deprived throughout the study. We used a highly preferred food item as incentive (banana pellet) that was not part of the daily diet. The apes had participated in multiple cognitive tests before the current study, some of which required inserting objects into tubes (e.g., Martin-Ordas & Call, 2009). All applicable international, national and institutional guidelines for animal behavioral research were followed.

Materials

The apparatus consisted of a transparent box (bonobos, gorillas: L 20 cm × W 20 cm × H 20 cm; chimpanzees, orang-utans: L 22 cm × W 21 cm × H 21 cm) with an opening at its lower end (L 18 cm × W 2.5 cm resp. 3 cm) and a tube (L 18.5 cm × W 5 cm) attached onto its top (Figure 1; see also Bird & Emery, 2009). Inside the box a platform was held parallel to the ceiling of the box by a magnet. The platform could be released by inserting a stone into the tube so that its weight collapsed the platform. Three stones were placed at each side of the apparatus on a protruding edge (distance: about 20 cm). We used plaster stones with the bonobos but then switched to PVC stones with two bonobos and to real stones with one bonobo (two bonobos bit pieces off the stones and one stopped exchanging them). Orang-utans, gorillas and chimpanzees were always tested with PVC stones. All stones used weighed between 15 and 20 grams and were originally grey (PVC, real stones) or painted grey with a non-poisonous color (plaster).

Procedure

In the baited condition, the apparatus was baited with a banana pellet except for one bonobo who preferred grapes over pellets. In the empty condition, the apparatus was left empty. Apes received four consecutive sessions with each of the conditions, counterbalanced for order across subjects. Groups were established by sorting apes into dyads (with regard to species, age and sex) and then randomly distributing them to the two groups (pseudo-randomization). We conducted one session per day which lasted 30 minutes maximum. A session comprised three trials with an inter-trial-interval of about two minutes, resulting in twelve trials per condition (like in von Bayern, Heathcote, Rutz, & Kacelnik, 2009). If subjects solved the task three times, or 30 minutes had passed, the session was finished. When subjects solved the task, they left the test room, the apparatus was re-baited and six stones were replaced. When subjects took stones with them, we did not exchange these for a food reward because we did not want subjects to establish a positive association with the stones. Thus, apes sometimes brought stones with them on consecutive trials which they possibly used to solve the task. All sessions were videotaped.

Analyses

We measured success (X out of 3 trials) and survival time (a combination of time passed and success) per session, as well as latency until success, latency until touching the stones, and manipulation time using INTERACT 9 (Mangold International). We further measured food-directed actions in the baited condition (i.e., manipulations at the tube hole, the lower box opening, directly above the reward or attempts to open the box by biting, hitting, or tearing) or manipulations at the respective locations of the apparatus in the empty condition using Solomon Coder (Péter, 2011). Latency until success and survival time started with first visual inspection. While latency could be established for successful individuals only, survival time could be determined for both successful and unsuccessful individuals. Survival time consists of a combination of how much time has passed (duration in frames) and if an event has occurred or not (success: yes or no). A second coder coded 20 percent of the videos and reliability was excellent (Pearson's correlation coefficient: success, $r = 1$, $df = 38$, $p < 0.001$; survival time, $r = 1$, $df = 38$, $p < 0.001$; latency to success, $r = 0.994$, $df = 26$, $p < 0.001$; manipulation, $r = 0.997$, df = 38, $p < 0.001$).

A generalized linear mixed model (GLMM) with a Poisson error structure was performed in R (R Core Team, 2013) with successful trials per session as the response (R-package lme4, Bates, Maechler, Bolker, & Walker, 2014). The model included group, condition, session, species, sex, age, and duration of stay at the holding facility as predictors, as well as the three-way-interaction between group, condition, and session. We used the duration that apes spent at our research facility as an additional variable as a proxy for apes' experience with cognitive studies. For apes who were born at the holding facility, we counted the months from their third birthday on because apes started to participate in studies around this age. Age was log-transformed and age, session as well as duration of stay at the holding facility were standardized to their respective means. As random effects the random intercept of subject and the random slopes of condition, session, and the product of condition and session within subject were included in the model (Barr, Levy, Scheepers, & Tily, 2013; Schielzeth & Forstmeier, 2009). We tested the overall effect of the predictors by comparing the full model with the null model comprising only the random effects employing a likelihood ratio test (Schielzeth & Forstmeier, 2009; R function anova with argument test set to "Chisq"). As a next step, non-significant interactions were excluded from the model (group x condition x session, $\chi^2 = 2.05$, $df = 1$, $p = 0.152$; group x condition, $\chi^2 = 0.58$, $df = 1$, $p = 0.445$; group x session, $\chi^2 = 0.12$, $df = 1$, $p = 0.730$) and *p*-values for the individual predictors were established using likelihood ratio tests comparing the full with the respective reduced models (Barr et al., 2013; R function drop1). To further investigate significant interactions, we re-leveled the respective factors involved.

We assessed model stability by visually inspecting the estimates derived by a model based on all data with those obtained from models with levels of the random effects excluded one at a time. Model stability was considered acceptable when the results did not change considerably compared to the results based on the entire dataset. Variance Inflation Factors (VIF, Field, 2005) were derived using the function vif of the R-package car (Fox & Weisberg, 2011) applied to a standard linear model excluding random effects and interactions, and did not indicate collinearity to be an issue. Overdispersion did not appear to be a problem (dispersion parameter: 0.331). We established confidence intervals (CIs) by parametric bootstrapping (R function bootMer from the package lme4) and assessed an R^2-like effect size (‘marginal’ R^2, the variance explained by the fixed effects).

For further analyses, we excluded six subjects who did not solve the task because we were interested in how the conditions modulate problem-solving performance of those who knew how to solve it. We also excluded the two remaining gorillas who caused a problem of complete separation in the model, resulting in a sample comprising seven bonobos, four chimpanzees and six orang-utans. A Cox mixed model with survival time as the response was performed in R (Therneau, 2012). The model included the same fixed and random effects structure as before but additionally, the interaction of species and condition was added. We tested the overall effect of the predictors by comparing the full with the null model comprising only the random effects, employing a likelihood ratio test which was based on the “integrated” likelihood provided by the function “coxme”. We established *p*-values for the individual predictors using again likelihood ratio tests comparing the full with the respective reduced models. We examined significant interactions by re-leveling the respective factors. Model stability was assessed the same way as in the GLMM for number of successful trials per session and was acceptable.

We analyzed how apes from the two groups reacted to the two conditions by analyzing their behavior in the first trial of each of the conditions. Only individuals who were successful in both first trials were included, resulting in a sample comprising five bonobos, three chimpanzees and six orang-utans. We conducted four linear mixed models (LMMs) with latency until success, latency until touching the stones, manipulation time and food-directed actions as the response. All four responses were log-transformed. Each model included the interaction between group and condition as well as the random intercept of subject. We established *p*-values in the same way as it was done in the GLMM for number of successful trials per session. We assessed normal distribution and homogeneity of the residuals by plotting the residuals (i.e., conducting a qq-plot and plotting residuals against fitted values) and they were rated good for all four models. VIFs did not indicate collinearity to be an issue and model stability for the four models was acceptable. CIs and effect sizes were established as in the Poisson model.

Results

Success

Seventy-six percent of the great apes solved the task at least once (seven bonobos, four chimpanzees, two gorillas and six orang-utans). Most of these apes solved the task in both conditions with the exception of three apes (one bonobo and two gorillas) from the empty-first group who solved the task in the baited condition only. Also, one bonobo from the baited-first group solved the task (twice) in the empty condition only. Six apes (one bonobo, three chimpanzees, and two gorillas) did not solve the task at all (see SOM for more details).

Figure 2 presents the success as a function of condition and group. The full model was significant compared to the respective null model (GLMM; likelihood ratio test: $\chi^2 = 59.53$, $df = 13$, $p < 0.001$; 'marginal' $R^2 = 0.49$). We found the interaction of condition and session to be significant ($\chi^2 = 10.00$, $df = 1$, $p = 0.002$). Exploring the interaction further revealed that apes' success declined over sessions in the empty condition ($p < 0.001$) while it stayed at high levels in the baited condition. While there was a general decline in the empty condition, there was remarkable variation among individuals in this condition and some apes continued dropping stones (success in the empty condition, mean: 31 %, minimum: 0 %, maximum: 92 %). We did not find an effect of group, that is, apes' performance was not dependent on the order of presentation of the two conditions ($\chi^2 = 0.15$, $df = 1$, $p = 0.702$). We observed a significant effect for age with older individuals being less successful ($\chi^2 = 4.76$, $df = 1$, $p = 0.029$). The duration of the stay at the holding facility revealed significance with those apes who arrived more recently being less successful ($\chi^2 = 19.89$, $df = 1$, $p < 0.001$). Neither sex ($\chi^2 = 0.16$, $df = 1$, $p = 0.688$), nor species ($\chi^2 = 5.56$, $df = 3$, $p = 0.135$) influenced apes' performance. See Table 1 for the results of the individual predictors.

A closer inspection of the factors age and duration of the stay at the holding facility revealed that their effect was probably driven by the six apes who completely failed the task. To investigate the influence of the two factors on apes' problem-solving performance more closely, we excluded these six apes and repeated the analysis. The influence of the duration of stay at the holding facility ceased to be significant ($\chi^2 = 1.08$, $df = 1$, $p = 0.298$) and the age effect became a trend into the opposite direction with older subjects tending to be more successful ($\chi^2 = 3.48$, $df = 1$, $p = 0.062$). However, one must be cautious in comparing these two models directly as excluding a fourth of the sample constitutes a substantial change.

Latencies

Figure 3 presents the survival time as a function of condition and group. The full model was significant compared to the respective null model (Cox mixed model; likelihood ratio test: $\chi^2 = 70.67$, $df = 14$, $p < 0.001$). We found a significant three-way interaction between group, condition and session ($\chi^2 = 8.40$, $df = 1$, $p = 0.004$). Exploring the interaction further revealed that apes from the baited-first group showed opposite patterns for the two conditions: they became faster over sessions in the baited condition ($p < 0.001$; see also SV1, SV2, SV4 and SV5) and slower over sessions in the empty condition ($p < 0.001$). Apes from the empty-first group also became slower over sessions in the empty condition ($p = 0.028$) but they did not show a decline in survival time in the baited condition as they solved the task quickly from the first trial onwards. Moreover, we found a significant interaction of condition and species ($\chi^2 = 7.00$, $df = 2$, $p = 0.030$). Exploring the interaction did not reveal a difference between the species except for one trend: orang-utans tended to solve the task more slowly than bonobos in the empty condition ($p = 0.077$). We found a trend for age with older subjects tending to solve the task more quickly than younger ones ($\chi^2 = 3.08$, $df = 1$, $p = 0.079$). Neither sex ($\chi^2 = 2.10$, $df = 1$, $p = 0.148$), nor duration of the stay at the holding facility ($\chi^2 = 0.54$, $df = 1$, $p = 0.462$) showed a significant influence. See Table 2 for the results of the individual predictors.

Figure 4A shows the latency until success in the first trials of each condition as a function of condition and group. The full model was significant compared to the null model (LMM; likelihood ratio test: $\chi^2 = 10.01$, $df = 3$, $p = 0.019$; 'marginal' $R^2 = 0.31$). We found a significant interaction between group and condition ($\chi^2 = 6.40$, $df = 1$, $p = 0.011$). Exploring the interaction further revealed that apes from the baited-first group took longer to solve the task in the baited condition than apes from the empty-first group ($p = 0.002$) while there was no such difference between groups in the empty condition. Apes from the baited-first group also took longer to solve the task for the very first time than apes from the empty-first group (session 1; $p = 0.011$; see also SV1, SV3, SV4 and SV6) while there was no such difference between the two groups when they switched to the respective other condition (i.e., session 5). Moreover, apes from both groups tended to become faster from the first to the second condition that they received (baited-first group: $p = 0.056$; empty-first group: $p = 0.074$). See Table 3 for the results of the individual predictors.

Figure 4B shows the latency until touching the stones in the first trials of each condition as a function of condition and group. Apes did not differ with regard to this measurement (LMM; full-null-model comparison: likelihood ratio test, $\chi^2 = 2.31$, $df = 3$, $p = 0.510$). Besides latencies, we also investigated how much time subjects devoted to manipulating the apparatus in general and specifically at the food location (or the corresponding location in the case of the empty condition).

Apparatus exploration

Figure 5A shows manipulation time as a function of condition and group in the first trials of each condition. The full model was significant compared to the null model (LMM; likelihood ratio test: $\chi^2 = 15.63$, $df = 3$, $p = 0.001$; 'marginal' $R^2 = 0.44$). We found a significant interaction between group and condition ($\chi^2 = 13.86$, $df = 1$, $p < 0.001$). Exploring the interaction further revealed that apes from the baited-first group manipulated the apparatus more in the baited condition than apes from the empty-first group ($p < 0.001$) while apes from the empty-first group manipulated the apparatus more in the empty condition than apes from the baited-first group ($p = 0.037$). Apes from the baited-first group also manipulated the apparatus more than apes from the empty-first group when they were confronted with the apparatus for the very first time (session 1; $p = 0.017$) while there was no such difference between the two groups when they switched to the respective other condition (session 5). Finally, apes from both groups manipulated the apparatus less from the first to the second condition that they received (baited-first group: $p < 0.001$, empty-first group: $p = 0.044$). See Table 4 for the results of the individual predictors.

Figure 5B shows the duration of food-directed actions (or actions directed at the corresponding location in the case of the empty condition) as a function of condition and group in the first trials of each condition. The full model was significant compared to the respective null model (LMM; likelihood ratio test: $\chi^2 = 9.18$, $df = 3$, $p = 0.027$; 'marginal' $R^2 = 0.29$). We found a significant interaction between group and condition ($\chi^2 = 8.54$, $df = 1$, $p = 0.003$). Exploring the interaction further revealed that apes from the baited-first group showed more food-directed actions in the baited condition than apes from the empty-first group ($p = 0.010$) and apes from the empty-first group tended to show more such actions in the empty condition than apes from the baited-first group ($p = 0.092$). Moreover, apes from the baited-first group showed more food-directed actions in the first compared to the second condition that they received (session 1; $p = 0.012$) while this was only a trend for apes from the empty-first group (session 5; $p = 0.079$). See Table 5 for the results of the individual predictors.

Furthermore, we explored the relative time that apes from the four species manipulated the apparatus with their hands and mouths ($N = 25$). We found a different pattern for the two conditions (LMM; full-null-model comparison, likelihood ratio test: $\chi^2 = 17.86$, $df = 7$, $p = 0.013$; likelihood ratio test for species x condition: $\chi^2 = 9.41$, $df = 3$, $p = 0.024$): while there was no species difference in the baited condition, orang-utans manipulated the apparatus significantly longer than the other species in the empty condition ($p = 0.028$). Additionally, bonobos manipulated the apparatus significantly longer in the baited than in the empty condition ($p < 0.001$) whereas there was no difference between conditions for the other ape species (baited – bonobos: 12±12%; chimpanzees: 9±12%; gorillas: 12±15%; orang-utans: 14±14%; empty – bonobos: 3±6%; chimpanzees: 4±6%; gorillas: 1±1%; orang-utans: 13±15%; percent of time manipulating the apparatus with hand or mouth, mean±sd.; Figure S1A and videos SV1-6; please see SOM for more details). Additionally, we found a significant difference between conditions with regard to tool-use: apes manipulated the apparatus significantly longer with stones in the baited than in the empty condition (LMM; full-null-model comparison, likelihood ratio test: $\chi^2 = 21.38$, $df = 7$, $p = 0.003$; likelihood ratio test for condition: $\chi^2 = 18.64$, $df = 1$, $p < 0.001$) while there was no effect of species ($\chi^2 = 2.65$, $df = 3$, $p = 0.448$; baited – bonobos: 13±15%; chimpanzees: 11±13%; gorillas: 6±9%; orang-utans: 13±12%; empty – bonobos: 3±6%;

chimpanzees: 3±9%; gorillas: 0±0%; orang-utans: 3±5%; Figure S1B, Table S2 and videos SV1-6; please see SOM for more details).

Discussion

When apes encountered the collapsible platform task for the first time, they solved it more quickly when the apparatus was empty than when it was baited, indicating that the presence of a food reward retarded the use of a stone to collapse the platform. Subjects starting with the baited apparatus also increased their opening speed over time in this condition while subjects who had already experienced the empty apparatus solved it quickly from the first baited trial onwards (and did not change over time). This suggests that prior experience with the empty apparatus increased problem-solving performance. Apes facing the baited apparatus first directed their manipulations towards the food location while this behavior was dramatically reduced in subjects who had already gained experience with the empty apparatus, demonstrating that experience with the empty apparatus equaled out the distracting effect of the food reward. These findings suggest that experience with the functional affordances of the setting narrowed down the manipulative focus to the relevant parts of the apparatus. Although most subjects opened the apparatus at least once regardless of the condition, they were more likely to continue to open it when it was baited than when it was empty. Subjects' latency to open the empty apparatus increased over time, showing that intrinsic motivation alone could not keep up performance without a food reward present. There were marked individual differences in the likelihood of continuing to open the apparatus in the empty condition, suggesting individually variable levels of intrinsic motivation to engage with an apparatus in a non-rewarded situation.

This study suggests that apes open a puzzle box more quickly in a non-rewarded situation compared to a rewarded one when encountering the puzzle box for the first time. Yet, repeated exposure to the empty apparatus reduced apes' overall success (and increased the latency) in this study which quickly recovered as soon as the apparatus was baited. One possible explanation for these results may also be found in the modulating effect of motivation. When initially faced with food inside the apparatus, individuals displayed direct but ineffective actions aimed at obtaining the food, such as inserting their fingers through the opening. Our finding is consistent with studies showing that a high extrinsic motivation decreases problem-solving performance (Birch, 1945b; Boysen & Berntson, 1995; Glucksberg, 1964; Suedfeld, Glucksberg, & Vernon, 1967; Vlamings, Uher, & Call, 2006). For example, chimpanzees performed better in several problem-solving tasks when they were in a state of medium food motivation compared to when it was low or high (Birch, 1945b). In a high state of food motivation they also persevered longest with their original solution strategy even if better ones were available, suggesting a strong focus onto the food (Birch, 1945b; see also Boysen & Berntson, 1995; Vlamings et al., 2006). In the current study, persistence in a rather narrow action search may have prevented the emergence of more indirect solutions, which is precisely what the task required (picking up a seemingly unrelated stone and dropping it into the tube). This explanation fits with our data on the time spent trying to directly access the food. Reducing the extrinsic motivational (by removing the food from the apparatus) may have allowed the emergence of those more indirect actions. However, for this to work, two requirements must be met: 1) the solution has to be within the subjects' repertoire and 2) subjects must be intrinsically motivated to manipulate the empty apparatus. In fact, these requirements were not apparent in a minority of subjects who consistently failed the task.

The current study demonstrates that exploration, even when it is not accompanied by extrinsic benefits, improves apes' problem-solving efficiency. Apes who experienced the empty apparatus subsequently solved the baited apparatus in a more efficient manner. This is consistent with other studies showing that non-human primates as well as human children learn about action-outcome contingencies in non-rewarded situations and use this knowledge subsequently in a problem-solving task (Birch, 1945a; Polizzi di Sorrentino et al., 2014; Taffoni et al., 2014). By manipulating the empty apparatus, apes in the current study seemingly extracted information about the affordances of the apparatus (e.g., its openings), its relation with other elements of the task (stones) and perhaps even the effect that dropping stones through the upper opening had on the collapsing platform. Although it is unclear how many of these pieces of information they acquired that later facilitated opening the baited apparatus, they did so by free exploration. Our results are consistent with previous studies demonstrating that diversity of exploratory actions increases problem-solving success in various animal species (e.g., Benson-Amram & Holekamp, 2012; Benson-Amram et al., 2013; Griffin et al., 2014; Griffin & Guez, 2014; Visalberghi & Fragaszy, 1989). While these studies show the effect of exploration in the presence of food rewards, our study also investigated the role of exploration without any food reward present and its impact on subsequent problem-solving, adding an important aspect to the phenomenon. Non-human great apes are well known for their strong exploratory tendency with novel objects (Forss, Schuppli, Haiden, Zweifel, & van Schaik, 2015; Glickman & Sroges, 1966; Tomasello & Call, 1997; Torigoe, 1985; Welker, 1956), although they show much higher rates of exploration in captivity than in the wild, as is the case for many animal species (Benson-Amram et al., 2013; Forss et al., 2015). Great apes show many and diverse object manipulations and are considered flexible tool-users so that it would not be surprising if they used their knowledge gained during free exploration in future problem-solving situations (Call, 2013).

One of the goals of the current study was to assess whether problem-solving influenced subsequent exploration. Apes from both experimental groups increased the time to solution across successive sessions in the empty condition, and there was no difference between the two groups in the first trial of the empty condition concerning latency until success. These findings suggest that prior experience with the baited apparatus did not influence apes' performance in the empty condition subsequently. We further found that apes from both groups manipulated the apparatus more in the first then the second condition that they received, indicating a general effect of experience. In the baited condition, this very likely indicates that they became proficient at extracting the food while in the empty condition this is likely to reflect a decrease in interest. Interestingly, those individuals who had already solved the baited condition spend less time manipulating the apparatus in the empty condition than those who had only been exposed to the empty condition. In other words, having solved the task seemed to suppress to some extent the amount of time that individuals devoted to manipulating an empty apparatus.

The collapsible platform task was originally developed to study rooks. In a study by Bird and Emery (2009), these animals succeeded in the task, but they needed to observe the consequences that their or others' actions had on the platform when the stone fell onto it. Although initially rooks did not collect tools to collapse the platform, they did so as soon as they discovered the effects that stones had on the platform. And once they had done so they displayed a remarkable ability to select appropriate tools that varied in terms of size and weight to solve the task. Similarly, New Caledonian crows solved the collapsible platform task, but they required additional information about the apparatus (von Bayern et al., 2009). Nevertheless, it is difficult to directly compare those two corvid species with the results of the current study partly because although our apes had never faced the collapsible platform apparatus, they had inserted tokens, water, or tools inside tubes to obtain rewards. This experience, however, should not be equated with having solved the current task. Otherwise it would be hard to explain why they did not solve the task right away, and the reason for the differences between conditions and individuals. It is true that the six apes who did not solve the task had less experience with tasks in general than successful subjects, but they were also either rather young or quite old and therefore we cannot be sure whether a lack of experience caused their failure (see also Manrique & Call, 2015). A recent study found that some naïve chimpanzees solved the collapsible platform task even though they lacked the experience of the apes included in the current study (Schmelz et al., unpublished data). Furthermore, another study suggested that orang-utans who regularly participated in cognitive studies performed at similar levels as orang-utans without such experience in several tasks on physical cognition (Forss & van Schaik, 2014; see also Forss, Willems, Call, & van Schaik, 2016). At least in that study, prior experience with experimental tasks did not increase subjects' performance compared to naïve individuals.

We found large individual differences with regard to the time spent manipulating the empty apparatus that may reflect differences in intrinsic and even extrinsic motivation. While some apes continued to drop stones into the tube and to manipulate the apparatus, others stopped these activities after a shorter period of time. This variability may reflect consistent individual differences in exploratory tendencies that have been found in great apes and other animal species (e.g., Uher et al., 2008; Zampachova et al., 2017), although we have no evidence of its temporal stability from this study. Also individual levels of persistence may account for apes' variability in the empty condition. However, two types of persistence may be involved here. Apes first facing the empty condition may have been persistent in exploring the apparatus due to an intrinsic motivation. However, apes who first encountered the baited apparatus potentially exhibited a carry-over effect in the empty condition because they had been extrinsically rewarded for the solution before. Here, persistence may reflect an extrinsic motivation. Interestingly, the distribution of apes with regard to the number of stones they dropped into the tube in the empty condition was similar for both groups, suggesting that after an initial phase of potential extrinsic motivation at least some apes might have been intrinsically motivated to explore the apparatus further. Persistence is thought to be an essential component of flexible problem-solving (e.g., Benson-Amram & Holekamp, 2012; Chow, Lea, & Leaver, 2016; Griffin et al., 2014; Huebner & Fichtel, 2015; Manrique, Völter, & Call, 2013). However, persistence alone may be insufficient in some situations unless it appears in combination with the use of different actions (i.e., exploration). For example, if we had disabled the original solution (e.g., by blocking the opening of the tube) and had provided a novel one (e.g., pressing down the platform through a hole at the side), persistence in manipulating the apparatus would have only worked if individuals also had explored alternative ways to access the reward (Auersperg, von Bayern, Gajdon, Huber, & Kacelnik, 2011; Manrique et al., 2013). Thus, those individuals exhibiting high levels of exploration in the empty condition may have the potential to be the best problem-solvers. To test this, one probably would have to use a task with a greater level of difficulty than the current one in which most apes did relatively well.

In conclusion, our data confirmed that exploration in a non-rewarded situation can enhance future problem-solving performance in non-human great apes. But additionally, we observed that problem-solving narrowed the type of exploration that individuals did after solving the task to obtain a food reward. This means that the relation between exploration and problem-solving is bidirectional. Another aspect of this study was the modulatory effect of extrinsic and intrinsic motivation on performance. Extrinsic motivation initially hindered the discovery of a solution but eventually aided it in sustaining performance over time after a solution was found. Such sustained performance could not be apparently maintained by an intrinsic motivation alone. Nevertheless, even in the baited condition subjects managed to solve the task, which means that the effect of motivation was not so strong as to completely prevent the appearance of the solution. It is conceivable that confronted with a greater incentive or a more difficult apparatus, prior experience might have been the key to success. One could say that while the intrinsic motivation provided the ignition for the acquisition process, extrinsic motivation subsequently fueled it on the longer run.

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Table 1. Results for the individual predictors for the model with success as the response.

Term	**Estimate**	**SE**	**lowerCL**	**upperCL**	χ^2	**Df**	**P**
Intercept	0.510	0.383	-0.357	1.274	(4)	(4)	(4)
Condition (empty) (2)	-1.071	0.229	-1.643	-0.666	(4)	(4)	(4)
Session (1)	0.007	0.070	-0.131	0.145	(4)	(4)	(4)
Group (baited first) (2)	0.150	0.392	-0.675	1.002	0.15	1	0.702
Species (chimp) (2)	-1.050	0.551	-2.332	0.012	5.56 (3)	3 (3)	0.135 (3)
Species (gorilla) (2)	-0.964	0.586	-2.304	0.181	(4)	(4)	(4)
Species (orang) (2)	-0.187	0.461	-1.182	0.791	(4)	(4)	(4)
Sex (male) (2)	0.161	0.403	-0.679	1.041	0.16	1	0.688
Age (1)	-0.519	0.251	-1.122	-0.055	4.76	1	0.029
Duration of stay (1)	1.094	0.283	0.622	1.811	19.89	1	<0.001
Condition (empty) (2) x Session (1)	-0.411	0.131	-0.708	-0.157	10.00	1	0.002

(1) log-transformed (age), standardized to its mean (age, duration of stay, session)

(2) reference categories: condition (baited), group (empty first), species (bonobo), sex (female)

(3) overall effect of the predictor (species)

(4) not shown because of having a very limited interpretation

Table 2. Results for the individual predictors for the model with survival time as response.

Term	**Estimate**	**SE**	χ^2	**Df**	**P**
Group (baited first) (2)	-1.347	0.894	(4)	(4)	(4)
Condition (empty) (2)	-3.232	0.617	(4)	(4)	(4)
Session (1)	0.013	0.199	(4)	(4)	(4)
Species (chimp) (2)	1.319	1.360	(4)	(4)	(4)
Species (orang) (2)	-0.204	0.891	(4)	(4)	(4)
Sex (male) (2)	-1.106	0.752	2.10	1	0.148
Age (1)	1.083	0.612	3.08	1	0.079
Duration of stay (1)	-0.505	0.707	0.54	1	0.462
Group (baited first) x Condition (empty) (2)	0.706	0.669	(4)	(4)	(4)
Group (baited first) x Session (1,2)	1.077	0.282	(4)	(4)	(4)
Condition (empty) x Session (1,2)	-0.699	0.368	(4)	(4)	(4)
Condition (empty) x Species (chimp) (2)	0.701	0.846	7.00 (3)	2 (3)	0.030 (3)
Condition (empty) x Species (orang) (2)	2.093	0.741	(4)	(4)	(4)
Group (baited first) x Condition (empty) x Session (1,2)	-1.662	0.545	8.40	1	0.004

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(1) log-transformed (age), standardized to its mean (age, duration of stay, session)

(2) reference categories: group (empty first), condition (baited), species (bonobo), sex (female)

(3) overall effect of the interaction (condition x species)

(4) not shown because of having a very limited interpretation

Table 3. Results for the individual predictors for the model with latency to success in the first trials as the response.

Term	**Estimate**	**SE**	**lowerCL**	**upperCL**	χ^2	**Df**	**P**
Intercept	2.272	0.466	-4.697	8.315	(2)	(2)	(2)
Group (baited first) (1)	2.263	0.659	-6.924	12.075	(2)	(2)	(2)
Condition (empty) (1)	1.197	0.634	-0.040	2.485	(2)	(2)	(2)
Group (baited first) x Condition (empty) (1)	-2.482	0.896	-4.168	-0.707	6.40	1	0.011

(1) reference categories: group (empty first), condition (baited)

(2) not shown because of having a very limited interpretation

Table 4. Results for the individual predictors for the model with manipulation in the first trials as the response.

Term	**Estimate**	**SE**	**lowerCL**	**upperCL**	χ^2	**Df**	**P**
Intercept	1.308	0.435	0.425	2.191	(2)	(2)	(2)
Group (baited first) (1)	2.350	0.615	1.102	3.599	(2)	(2)	(2)
Condition (empty) (1)	1.286	0.615	0.038	2.535	(2)	(2)	(2)
Group (baited first) x Condition (empty) (1)	-3.685	0.870	-5.450	-1.919	13.86	1	<0.001

(1) reference categories: group (empty first), condition (baited)

(2) not shown because of having a very limited interpretation

Table 5. Results for the individual predictors for the model with duration of food directed actions in the first trials as the response.

Term	**Estimate**	**SE**	**lowerCL**	**upperCL**	χ^2	**Df**	**P**
Intercept	0.639	0.442	-0.243	1.525	(2)	(2)	(2)
Group (baited first) (1)	1.712	0.625	0.483	2.897	(2)	(2)	(2)
Condition (empty) (1)	1.130	0.625	-0.106	2.350	(2)	(2)	(2)
Group (baited first) x Condition (empty) (1)	-2.792	0.884	-4.485	-1.032	8.54	1	0.003

(1) reference categories: group (empty first), condition (baited)

(2) not shown because of having a very limited interpretation

Figure 1. The task required apes to drop a stone into a tube to release a platform inside the apparatus.

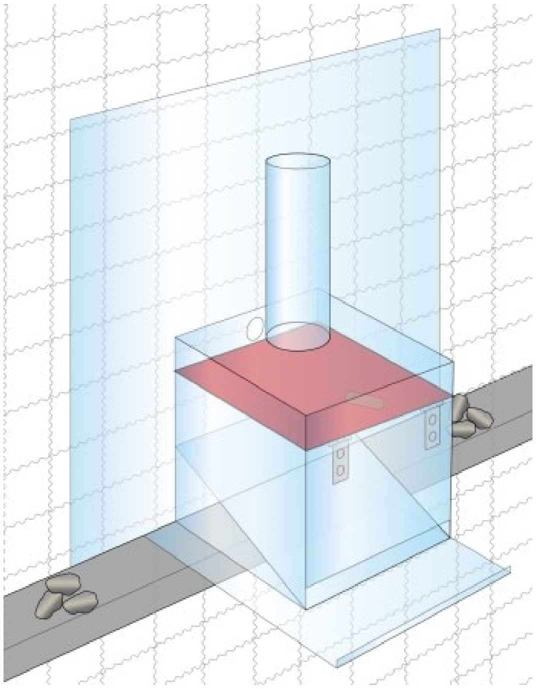

Figure 2. Mean number of successful trials per session in the baited (A) and the empty condition (B) as a function of group and session.

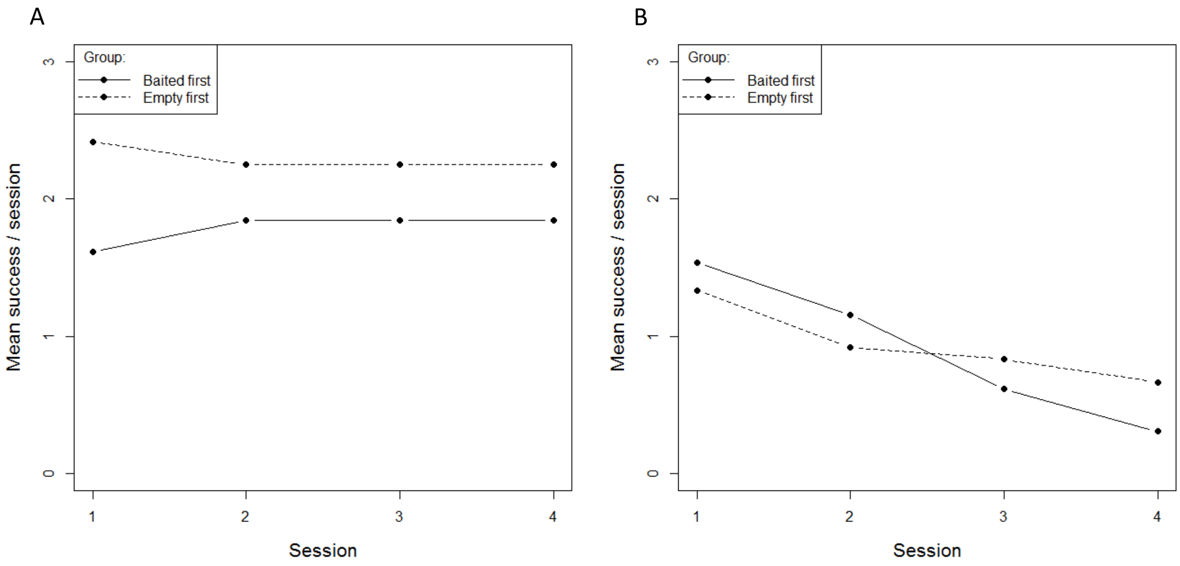

Figure 3. Latency to success in the baited (A) and the empty condition (B) as a function of group and session. Please note that we plotted latencies only here for reasons of visualization, yet, the survival time is a compound of success and latency. Grey: baited-first group, white: empty-first group (median; boxes: 0.25, 0.75; whiskers: 0.025, 0.975)

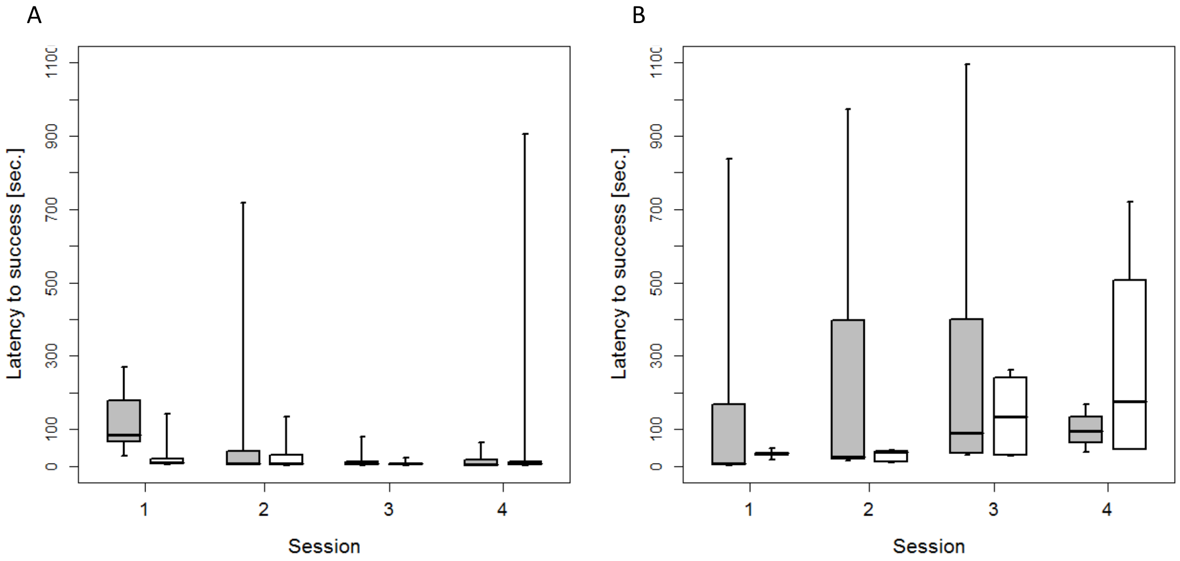

Figure 4. Latency to success (A) and latency to touch the stones (B) as a function of condition and group in the first trial of each condition. Grey: baited-first group, white: empty-first group (median; boxes: 0.25, 0.75; whiskers: 0.025, 0.975)

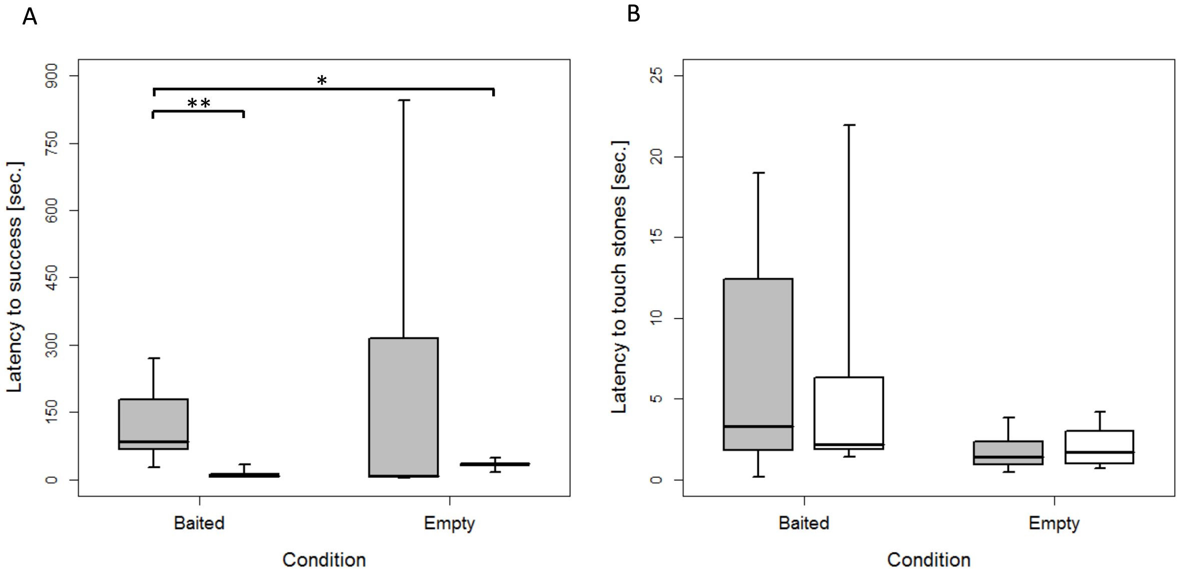

Figure 5. Manipulation time (A) and more specifically, food-directed actions (B) as a function of condition and group in the first trial of each condition. Grey: baited-first group, white: empty-first group (median; boxes: 0.25, 0.75; whiskers: 0.025, 0.975)