Inhibitory control and cue relevance modulate chimpanzees' (*Pan troglodytes*) performance in a spatial foraging task

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Abstract

Inhibition tasks usually require subjects to exert control in order to act correctly when a competing action plan is pre-potent. In comparative psychology, one concern about the existing inhibition tasks is that the relative contribution of inhibitory control to performance (as compared to learning or object knowledge) is rarely explicitly investigated. We addressed this problem by presenting chimpanzees with a spatial foraging task in which they could acquire food more efficiently by learning which objects were baited. In Experiment 1, we examined how objects that elicited a prepotent approach response, transparent cups containing food, affected their learning rates. While showing an initial bias to approach these sealed cups with visible food, the chimpanzees learned to avoid them more quickly across sessions compared to a colour discrimination. They also learned a colour discrimination more quickly if the incorrect cups were sealed such that a piece of food could never be hidden inside them. In Experiment 2, visible food of two different types was sealed in the upper part of the cups: one type signalled the presence of food rewards hidden underneath; the cups with the other type were sealed. The chimpanzees learned more quickly in a congruent condition (the to-be-*chosen* food cue matched the reward), than in an incongruent condition (the to-be-*avoided* food cue matched the reward). Together these findings highlight that performance in inhibition tasks is affected by several other cognitive abilities such as object knowledge, memory, and learning, which need to be quantified before meaningful comparisons can be drawn.

Keywords: inhibitory control, executive functions, reinforcement learning, comparative psychology, object representation, cylinder task

Inhibitory control and object knowledge modulate chimpanzees' (*Pan troglodytes*) performance in a spatial foraging task

In comparative psychology, there is growing interest in explaining variation in task performance (Boogert, Madden, Morand-Ferron, & Thornton, 2018; Johnson-Ulrich et al., 2018; Müller et al., 2016). Inhibitory control has been proposed as a critical factor explaining species differences (Amici, Aureli, & Call, 2008; MacLean et al., 2014). It is an attractive idea as it could help to explain domain-general differences in the cognitive abilities between species (referred to as G factor, see Burkart, Schubiger, & van Schaik, 2016). MacLean and colleagues (2014), for example, found evidence that absolute brain size predicted variation across species in a compound score of two inhibition tasks. Moreover, performance across the two inhibition tasks was correlated across species. However, the underlying assumption seems to be that inhibitory control is a unitary, domain-general cognitive ability that can empirically be distinguished from other executive functions, but neither the human psychometric literature (Duckworth & Kern, 2011; Friedman & Miyake, 2004; Nigg, 2000, 2017) nor evidence from comparative research supports this notion (van Horik et al., 2018; Völter, Tinklenberg, Call, & Seed, 2018). Indeed, a re-analysis of the MacLean et al. data found no evidence for a correlation of task performance across the two administered inhibition tasks at the level of the individual (Völter et al., 2018).

Tasks aiming at measuring inhibitory control (henceforth: inhibition tasks) typically require the subject to choose a novel action in a context associated with another prepotent action plan. That is, the starting point for any assessment of inhibitory control has to be some kind of prepotent response that needs to be overridden. Following Nigg (2000; 2017), we might categorize inhibition tasks according to the way the prepotent action is established: *interference control* tasks involve suppressing a distractor stimulus that triggers a prepotent response (e.g., in the Stroop colour-naming task in which participants need to name the ink colour of colour words instead of the colour denoted by the words), and *intentional motor inhibition* tasks involve the control over motor responses following changes in the context (e.g. in go/no-go paradigms, or reversal learning tasks). In the former, interference control tasks, the stimulus triggers a prepotent response because it has an inherently attractive quality (e.g. reaching directly for a visible piece of food behind a transparent obstacle). In the latter case, the response gains its prepotency over the course of the experiment, through many repetitions of an action often under time pressure (e.g., pressing keys as fast as possible in response to a stream of stimuli on a screen).

Reversal learning resembles the intentional motor response task in that the prepotent response is created by repeated exposure to a response-outcome or stimulus-response association. In the test phase, these contingencies are then reversed and adaptive responding to the new contingencies is measured. Even though reversal learning has been traditionally considered as a primary measure of inhibitory control (Jones & Mishkin, 1972) more recently other contributing factors such as the formation of learning sets (i.e., acquired rules that allow for faster learning of successive discriminations) or the representation of task space have been highlighted (Izquierdo, Brigman, Radke, Rudebeck, & Holmes, 2017).

In the comparative literature, examples of interference control tasks include detour-reaching tasks in which food is usually placed behind a transparent screen or inside a transparent cylinder (e.g., Amici et al., 2008; Bray, MacLean, & Hare, 2014; Gurgand & Beran, 2021; MacLean et al., 2014; van Horik et al., 2018; Vlamings, Hare, & Call, 2010). The prepotent response in this case is to reach directly for the food, resulting in bumping into the transparent screen. Sometimes bumping into the screen leads to the loss of the food reward (in the case of swing-door paradigms; Amici et al., 2008; Vlamings et al., 2010), in other cases it imposes a delay in its attainment (as in the transparent cylinder task). We have argued elsewhere (Völter et al., 2018) that this method is problematic in a comparative framework because of the well-known 'task impurity' problem: factors other than inhibition can affect performance (e.g., experience with or proclivity to learn about the object properties involved). It remains unclear whether an unsuccessful animal or group of animals is bad at inhibitory control, or if the task is bad at measuring the ability in this case (Kabadayi et al., 2017).

The most widespread example of an intentional motor inhibition task in the comparative literature is the A-not-B error paradigm. In this paradigm, individuals repeatedly witness how a food reward is hidden in location A, before it is moved to location B in full view of the participant on the test trial (Amici et al., 2008; Barth & Call, 2006; MacLean et al., 2014). Choosing hiding place A, the A-not-B error, has been interpreted (at least in part) as failure to inhibit the previously reinforced action towards location A (Diamond, 1990; for an alternative account not involving inhibitory control processes, see Smith, Thelen, Titzer, & McLin, 1999). However, recent comparative evidence highlights that other factors can also influence performance in this task, such as training to follow the hand motions of a human experimenter (Jelbert, Taylor, & Gray, 2016). Again, the lack of a control or contrasting conditions where competence can be demonstrated has proved problematic for interpreting poor performance. In the A-not-B error paradigm, for example, one could manipulate the number of 'A' trials from one to many to examine systematic variation in performance related to this change in the strength of prepotency. However, this has rarely been done (for an exception, see Davis, 2017).

In the current series of experiments, our goal was to examine how performance on a 'visible food' interference control task compared with learning in the absence of a stimulus eliciting a prepotent-response. In previous studies, chimpanzees (*Pan troglodytes*) performed at or close to ceiling in detour reaching tasks with food behind a transparent obstacle (Amici et al., 2008; MacLean et al., 2014). This ceiling effect raises the concern that this task is unsuitable for testing inhibitory control in chimpanzees, because the prepotent response seems to be weak or absent. An exception is the swing-door paradigm in which the food is located behind a transparent flap door, which pushes the food out of reach when the participant tries to reach the food. A lack of understanding of the swing-door mechanism might make this task harder for chimpanzees. Interestingly, preschool children up to 5 years of age also find the latter task difficult (Gurgand & Beran, 2021; Vlamings et al., 2010). The performance in the swing-door task in comparison to other interference control tasks illustrates that multiple factors can influence performance on an inhibition task. A contributing factor might be the ability to anticipate the likely outcome of actions, perhaps due to experience with the objects involved. Without explicitly testing the impact of such factors, the proportion of variation explained by inhibitory control abilities remains unclear.

Chimpanzees also performed close to ceiling in the A-not-B error task (Amici et al., 2008; Barth & Call, 2006; MacLean et al., 2014). In delay of gratification tasks in which participants can choose between an immediate reward and a better but delayed reward, chimpanzees can wait for minutes for better rewards (e.g., Amici et al., 2008; Beran, 2002; Beran & Evans, 2006). However, the extent to which performance is influenced by other factors remains unclear from these studies. In the case of tasks delaying gratification (Beran, 2015; Völter et al., 2018), temporal discounting (i.e., a preference for immediate rewards over delayed higher-value rewards) is an important factor influencing performance. In the case of the A-not-B error, previous experience with certain experimental procedures (e.g., hand-tracking; Jelbert et al., 2016), or strength of object representations/ working memory, could render the task unsuitable because of a failure to induce prepotency (much as it would be unsuitable for testing humans over a certain age, for whom the task is trivially easy).

In our study, we therefore had two main aims: first, to establish the existence of a prepotent response (i.e., an initial preference for the incorrect option) and second, to compare the ability to learn an effective solution in the presence and absence of this response. We aimed to examine the whole acquisition curve over multiple trials, as opposed to taking a snapshot of performance using different materials over few trials as is typically done in the comparative literature. Neuro-cognitive research does not enforce a clear dichotomy between slow, effortful, executively controlled actions and fast, automatized, and learnt actions, but rather a continuum (Meier, Lea, & McLaren, 2018; Verbruggen, McLaren, & Chambers, 2014). Monitoring negative outcomes, response errors, and response conflicts are associated with overlapping brain areas in humans and monkeys in the posterior medial frontal cortex (Holroyd & Coles, 2002; Ridderinkhof, Ullsperger, Crone, & Nieuwenhuiss, 2004). Activation in these areas is also associated with subsequent short-term adjustments in performance. Interestingly, the same brain areas seem to be important for reinforcement learning in monkeys and humans. These findings raise the possibility that a common mechanism is responsible for the monitoring of negative outcomes relevant to both inhibition tasks and reinforcement learning.

In the current study, we examined how interference-inducing stimuli (transparent cups containing visible but inaccessible food) often used in inhibition tasks, would affect discrimination learning in chimpanzees compared with situations in which peripheral demands were matched but without the prepotent component. We presented zoo-housed chimpanzees with a spatial foraging paradigm, in which we distributed 24 cups on the floor of their enclosure, of two visually distinct types (12 of each). Only one type of cup contained accessible food rewards in a given session. In the inhibition condition, half of the cups were transparent containing visible food that was not accessible (because the cups were sealed), and half were opaque and contained accessible food. In the colour discrimination condition, both types of cups were opaque but each type was a different colour, only one of which was baited with food. We expected that the chimpanzees would show an initial preference for the transparent cups with visible food inside and examined how fast they would be able to learn to avoid these cups compared with the colour discrimination condition. Previous research provided evidence that chimpanzees show rather slow learning rates in colour discrimination tasks (Hanus & Call, 2011; Schrauf & Call, 2009) and excellent performance in detour-reaching tasks involving transparent materials (Amici et al., 2008; MacLean et al., 2014). This raises the possibility that chimpanzees would learn to avoid the interference-inducing stimuli more quickly than to discriminate between stimuli of different colours due to the larger prediction error in the former task (Den Ouden, Friston, Daw, McIntosh, & Stephan, 2008; Rescorla & Wagner, 1972). The prediction error can be defined as difference between the expected and experienced outcome, a difference that is central in inhibition tasks involving visible but inaccessible food. In the context of the current task, the subjects may expect to retrieve the food that they can see but then experience that, in fact, they cannot retrieve it; this mismatch between expectation and outcome is the driver of learning according to models of classical conditioning (Rescorla & Wagner, 1972).

The inhibition task has two dimensions that differ from a typical discrimination task: (1) the transparency of one stimulus type and (2) the fact that some cups are permanently sealed. When we initially observed faster learning rates in the inhibition task with its sealed, transparent distractors, we realised that faster learning rates could have resulted from the differences in prediction error triggered by the prepotent stimuli (visible food) – but also from the closed distractor stimuli if the chimpanzees were sensitive to the affordances of open and closed cups. Research with human infants showed that infants acquire expectations about the containment function of objects during the first year of life (Hespos & Baillargeon, 2006). Evidence from the wild (showing that chimpanzees fold leaves to use them as drinking tools; Tonooka, 2001) as well as the experience of these zoo-housed chimpanzees with drinking cups might indicate that they pay attention to this object property. To disentangle the effect of visible food and sealed distractors we therefore added the colour discrimination with sealed-distractor condition, predicting that this should be solved more quickly than the condition in which both cups were possible hiding places.

Finally, previous research with nonhuman apes suggested that younger adults outperform older individuals in tasks tapping into executive functions similar to findings with humans (Manrique & Call, 2015; Völter & Call, 2014). Based on these findings, we expected that younger adults would show faster learning rates than older individuals, particularly in the condition requiring inhibitory control.

Experiment 1

In this experiment, we compared an inhibition task in which subjects were to learn to avoid visible but inaccessible food items to a colour discrimination learning task without any such interference. A secondary manipulation concerned the object properties of the distractor stimuli: we manipulated whether the distractor cups were open at their bottom (and therefore suitable hiding places for the food rewards) or not.

Material and methods

Subjects. Thirteen chimpanzees (*Pan troglodytes*) participated in this experiment. The subjects were housed at the Wolfgang Köhler Research Centre, Leipzig Zoo (Leipzig, Germany). Our sample consisted of 7 females and 6 males aged between 6 and 40 years (M_{age} 23.7 years). The study complied with the European and World Associations of Zoos and

Aquariums Ethical Guidelines and was approved by the joint ethical committee of the Max Planck Institute for Evolutionary Anthropology and Leipzig Zoo. The chimpanzees were neither food nor water-deprived and could participate or refuse to participate in this study by their own choice. All individuals had participated in various cognitive experiments before this study including studies on inhibitory control (e.g., Amici et al., 2008; Vlamings et al., 2010). While all individuals had experience with transparent materials (e.g., with Plexiglas panels), to our knowledge, the chimpanzees had not manipulated sealed transparent containers with food items inside before the start of this study.

Design. We used a 2x2 design (task x baited cup): individuals completed two tasks, the inhibition and colour discrimination task, in counterbalanced order (see Figure 1 and Table 1). In the inhibition task (see Online Resource 2 for a video), accessible food items were either inside open and transparent cups (‘Choose Visible Food’ condition) or hidden under opaque (olive green) cups. In the latter condition with accessible food hidden under opaque cups, the transparent cups were sealed and contained inaccessible food rewards (‘Avoid Visible Food’ condition). In the colour discrimination task (see Online Resource 3), the food was either hidden underneath yellow or blue cups. There is evidence that chimpanzees have similar colour perception and colour classification to humans (Grether, 1940; Matsuzawa, 1985). We opted for a yellow/blue discrimination because previous studies suggested a less complete red-green differentiation in chimpanzees (Grether, 1940).

In each task, subjects first learnt that one of the stimuli contained accessible food (initial phase). After they had learnt the initial discrimination (criterion: 10 out of the first 12 lifted cups correct in two consecutive sessions) we reversed the contingency between stimuli and reward and trained them again to criterion. They then received the other task type, and a final reversal. The order of the task presentation (inhibition or colour discrimination first) was counterbalanced across subjects. In the inhibition task, the type of distractor object was manipulated within subject (as part of the initial and reversal test phase, see Figure 1b and c); in the colour discrimination task, the type of distractor cup was manipulated between subjects (i.e., the distractor cups were open or closed throughout both test phases). Subjects completed two sessions per day. Testing in each test phase ended when the subjects reached the aforementioned criterion or after a maximum of 20 sessions per task and test phase.

Setup and materials. We distributed 24 polycarbonate cups (height x diameter: 4 cm x 6 cm) on the floor of the enclosure on a 6x8 grid, which covered an area of 120 x 180 cm. The distance between adjacent cups on the grid was 20 cm. Small grey paint marks on the floor indicated the points of the 6x8 grid. There were always two types of cups, 12 per type (indicated by their colour or transparency). One type of cup always contained accessible food, the other one did not. The distribution of the cups on the grid was pseudo-random with the restriction that there were two cups of each type in any of the eight columns of the grid. The distribution of the cups changed from session to session.

In the inhibition task, there were 12 clear and 12 opaque (olive green) cups (see Figure 1a, b, and c). The clear cups always contained a visible food item. We used either half a grape or half a pellet (both food rewards had a diameter of approximately 2 x 2 cm and a height of 1.5 cm). The food types were randomly assigned to subjects and the assignment was maintained throughout the study. Two chimpanzees did not eat the grapes in their first 4 and 5 sessions, respectively. One of these chimpanzees started with the inhibition task, the other one with the colour discrimination task. We changed the rewards to pellets and excluded these initial sessions in which only few cylinders were touched from the data analysis. A previous food preference test provided evidence that the chimpanzees regarded both food types as high-value rewards but also that they preferred pellets over grapes (Sánchez-Amaro et al., 2016). We found no evidence that the type of food reward mattered for the chimpanzees' performance in the current task (Table S1).

In the 'Avoid Visible Food' condition, the clear cup was sealed (a base plate was glued to the cup by means of a transparent Plexiglas adhesive) and the food was inaccessible, and the green cup was baited. In the 'Choose Visible Food' condition, the clear cup was baited (and the base plate was not glued to the cylinder) and the green cup was empty. Therefore, in one condition the distractor cup was sealed and in the other both cups were open. To explore the impact of this difference there were two versions of the colour discrimination. In both versions, there were 12 yellow and 12 blue cups. In the 'Sealed Distractor' condition, the incorrect colour cup was sealed and could not be baited (as in the Avoid Visible Food condition). In the 'Both Open' condition, the incorrect colour cup was open, but never baited (as in the Choose Visible Food condition). After the initial discrimination, all participants received a reversal, in which the other kind of cup produced a reward.

Two cameras were used to videotape the chimpanzees' search behaviour. The position of the cameras can be seen in Figure 1*f*. One of the cameras had a wide-angle lens (GoPro) and was mounted to the wall inside the enclosure. The other camera was outside the enclosure behind a Plexiglas panel.

Procedure. Subjects were tested individually. At the beginning of a session, the chimpanzees entered the room with the array of 24 cups. Subjects could then interact with the cups and retrieve the food. A session lasted until the subject did not lift a cup for 1 minute or earlier if a subject threw the cups around without looking for the food (e.g. during dominance display). This happened in 16 sessions (3.4 % of all sessions). At the end of the session, subjects were moved to the adjacent compartment of the enclosure and the cups were set up one more time in a new spatial arrangement. While the experimenter set up the cups for the second session, an opaque screen was placed in between the array and the adjacent compartment that occluded the cups from the subjects' view.

Scoring and analysis. We scored the order and coordinates on the grid of the cups that were lifted by the subject, whether the cups were baited, and whether the subject had lifted the same cup before within the same session. Cups that were thrown around and not lifted or turned over one by one were not considered. We analysed the first 12 cups that were turned over per session (not considering repeated choices) regarding their baiting status (binary response). As 12 out 24 cups were accessible/baited, the proportion of accessible/baited cups that were lifted within the first 12 lifted cups per session could vary between 0 and 1. The datasets generated and analysed during the current study are available as part of the supplementary material (Online Resource 5).

A second coder naïve to the hypotheses and theoretical background of the study scored 20% of all choices to assess interobserver reliability which was excellent (baiting status of first 12 lifted cups: $K=0.96$, $N=384$, $p<0.001$; number of lifted cups per session: $r_S=0.95$, $N=32$, $p<0.001$).

We used a Generalized Linear Mixed Model (GLMM; Baayen, 2008) with binomial error structure and logit link function (McCullagh & Nelder, 1989) to analyse the first 12 lifted cups per session regarding their baiting status (coded as 1 if an accessible/baited cup was lifted and 0 if an inaccessible/empty cup was chosen).

Additionally, we fitted negative binomial models to analyse the count of the lifted cups within a session, including revisited cups, as a measure of perseveration.

We included subject ID as random effect. To keep type I error rate at the nominal level of 5% (Barr, Levy, Scheepers, & Tily, 2013; Schielzeth & Forstmeier, 2009), we included all possible random slope components (except for the correlation parameters among random intercepts and random slopes terms) of task, distractor condition, session, their interaction terms, reversal phase, order of tasks, and choice within subject ID. Prior to fitting the models, the covariates were standardised (to a mean of zero and a standard deviation of one) to make the estimates easier to interpret. We determined variance inflation factors (Field, 2005) for standard linear models excluding the random effects using the R package car (Fox & Weisberg, 2011). Collinearity was no issue (see Online Resource 1 for maximum Variance Inflation Factors (VIF) of every model). We assessed model stability by comparing the estimates derived from the model based on all data with those obtained from models with individual subjects (i.e., the levels of the random effects) excluded one at a time. This revealed the models to be stable with regard to the fixed effects.

As an overall test of the effect of the test predictors we compared the full models with a respective null model lacking the test predictors but comprising the same control predictors and random effects structure as the full model (Forstmeier & Schielzeth, 2011) using a likelihood ratio test (Dobson, 2002). P values for the individual effects were based on likelihood ratio tests comparing the full with respective reduced models (Barr et al., 2013; R function drop1 with argument 'test' set to "Chisq"). The model was implemented in R (version 3.3.2; R Core Team, 2016) using the functions glmer and glmer.nb of the R package lme4 (Bates et al., 2015). Confidence intervals for the binomial models were derived using the function bootMer of the R package lme4, using 1,000 parametric bootstraps and bootstrapping over the random effects.

Results

The chimpanzees learned more quickly in the inhibition task compared to the colour discrimination, and when the distractor cup was sealed compared to when it was open. In the inhibition task, subjects learned faster in the Avoid Visible Food condition than the Choose Visible Food condition.

Learning rates (correct choices within the first 12 visited cups). We first analysed how fast individuals learnt across the two tasks to lift the baited cups. We fitted a binomial model with choice correct as response variable and included the task (inhibition vs colour discrimination), distractor condition (open vs sealed distractor cup), session number within phase and task, and all 2 and 3-way interactions between these three predictor variables, phase (initial vs reversal learning), age, and sex as test predictors as well as order of the tasks (1-2) and choice number within session (1-12; i.e., the order of lifted cups) as control predictors (full-null model comparison: $\chi^2=101.50$, df=10, $p<0.001$; see Table S2 for a detailed model output). The interactions served to examine whether the chimpanzees would learn faster over sessions in one of the task conditions. If the presence of visible but inaccessible food in the Avoid Visible Food condition of the inhibition task makes learning particularly slow (due to the inhibition demands) or fast (due to the prediction error associated with this condition) we would expect such an interaction. If the chimpanzees, additionally, were sensitive to the suitability of the distractor cup as a hiding location, we expected 2-way interactions between task and session and distractor condition and session.

We found that the 3-way interaction between task, session, and the distractor condition was not significant ($\chi^2=0.23$, df=1, $p=0.630$). In a reduced model (GLMM 02; see Table S3) without the 3-way interaction (full – null model comparison: $\chi^2=97.32$, df=9, $p<0.001$), we found significant interactions between task and session ($\chi^2=13.29$, df=1, $p<0.001$) and distractor condition and session ($\chi^2=5.57$, df=1, $p=0.018$) but not between task and distractor condition ($\chi^2=0.49$, df=1, $p=0.485$): individuals reached the (80% correct) learning criterion more quickly in the inhibition task compared to the colour discrimination task (see Figure 2 and 3). Moreover, individuals presented with closed distractor objects (with a sealed bottom) exhibited faster learning rates compared to the open distractor condition (see below). Besides, in both tasks individuals performed better in the initial compared to the reversal learning phase (χ^2=18.76, df=1, *p*<0.001), younger individuals performed better than older ones (χ^2=6.21, df=1, *p*=0.013), and females performed better than males (χ^2=5.55, df=1, *p*=0.019). Choice number within session (χ^2=0.48, df=1, *p*=0.489) and the order of tasks (χ^2=0.60, df=1, *p*=0.440) had no significant effects on performance.

Based on the significant interactions we analysed the two tasks separately. In the inhibition task (GLMM 03; full-null model comparison: χ^2=34.18, df=6, *p*<0.001; see Table S4), we found that individuals learnt faster across sessions in the Avoid Visible Food condition than the Choose Visible Food condition (interaction: χ^2=5.67, df=1, *p*=0.017; see Fig. 2). Moreover, individuals learnt faster in the initial learning phase compared to the reversal phase (χ^2=4.28, df=1, *p*=0.039). There were no significant effects of age, sex, choice number within session, and order of conditions (all p-values > 0.1).

In the colour discrimination task (GLMM 04; χ^2=55.69, df=6, *p*<0.001; see Table S5) we found that individuals learnt faster across sessions in the Sealed Distractor condition compared to the Both Open condition (interaction: χ^2=5.38, df=1, *p*=0.020; see Fig. 3). Moreover, individuals learnt faster in the initial learning phase compared to the reversal (χ^2=15.30, df=1, *p*<0.001). Younger individuals performed better than older ones (χ^2=16.58, df=1, *p*<0.001) and females performed better than males (χ^2=12.35, df=1, *p*<0.001). There were no significant effects of choice number within session or the order of conditions (both p-values > 0.1).

First session performance in the initial learning phase. The chimpanzees had an initial preference for the clear cups with food inside: 10 out of 12 individuals lifted the clear cup in their first choice (binomial test: *p* = 0.038) and all chimpanzees who started with the inhibition task (N=7) first chose the clear cup (binomial test: *p* = 0.015). Moreover, the chimpanzees tried to break the closed clear cups with their teeth or by pounding them. However, already in the course of the first session the apes' performance in the Avoid Visible Food condition improved in contrast to the Choose Visible Food condition (see below). In their first choice in session 2, only 6 out of 12 individuals chose the transparent cup (p = 1) in the inhibition task; 11 out of 12 individuals chose the cup with accessible food (p = 0.006). In contrast, in the colour discrimination task the chimpanzees had no significant preference for one of the two colours in their first choice in session 1 (7 out of 12 individuals chose the blue cup; binomial test: p= 0.774; 6 out of 12 individuals chose the baited cup: p = 1). Moreover, there were no significant changes in performance within the first 12 choices of the first session in the colour discrimination task. In their first choice in session 2, 9 out of 12 individuals chose chose the cup with accessible food (p = 0.146).

In GLMM 05, we analysed learning rates within the first session of the initial learning phase across the two tasks. The model approached significance when compared to a null model lacking the test predictors (χ^2=16.60, df=9, p=0.055, see Table S6). There was a significant 3-way interaction between task, choice number, and the distractor condition (χ^2=6.15, df=1, p=0.013; see Fig. 4). Moreover, the younger individuals performed better than older ones (χ^2=4.39, df=1, p=0.036). The other predictor variables did not show any significant associations with first session performance (both p-values >0.1).

Following the significant interaction we analysed the two tasks separately. In the inhibition task (GLMM 06; full – null model comparison: χ^2=10.88, df=1, p=0.054, see Table S7), the interaction between choice number and condition approached significance (χ^2=3.69, df=1, p=0.055). Post-hoc tests showed that individuals tended to improve across choices in the Avoid

Visible Food condition (χ^2=3.36, df=1, p=0.067) but not in the Choose Visible Food condition (χ^2=0.60, df=1, p=0.437), in which they already performed well from the beginning. Moreover, younger individuals performed better than older ones (χ^2=6.32, df=1, p=0.012). In the colour discrimination task (GLMM 07), there were no significant effects of the predictor variables on the first session performance (full – null model comparison: χ^2=5.40, df=5, p=0.369).

Perseveration (number of lifted cups per session). As a measure of perseveration, we analysed the number of lifted cups (including re-visited cups) per session as dependent variable We included task and distractor, their interaction, the mean accuracy within the first 12 choices per session, session, reversal phase, sex, and age as test predictors as well as the order of tasks as control predictor (GLMM 8, full-null model comparison χ^2=55.11, df=7, p<0.001; see Table S8). We found a significant interaction between task and distractor (χ^2=18.20, df=1, p<0.001). With increasing accuracy within the first 12 unique choices, the total number of lifted cups per session declined (χ^2=16.32, df=1, p<0.001). There were no significant effects of phase (initial vs reversal; χ^2=2.86, df=1, p=0.091), session (χ^2=2.33, df=1, p=0.127), order of task (χ^2=0.17, df=1, p=0.679), sex (χ^2=0.67, df=1, p=0.414), or age (χ^2=2.11, df=1, p=0.146).

Based on the significant interaction we analysed the two tasks separately. In the inhibition task (GLMM 09; full-null model comparison: χ^2=39.39, df=5, p<0.001; see Table S9), we found that individuals lifted more cups per session with the closed clear cups with inaccessible food items inside compared to the open condition in which the accessible food was under the opaque cups (χ^2=22.26, df=1, p<0.001; see Figure 5*a*). Moreover, with increasing accuracy in the first 12 choices the number of lifted cups declined (χ^2=12.65, df=1, p<0.001). With increasing age individuals tended to lift more cups per session (χ^2=6.31, df=1, p=0.012). There were no other significant effects (all p-values > 0.1).

In the colour discrimination task (GLMM 10; full-null model comparison: $\chi^2=23.38$, df=5, $p<0.001$; see Table S10), we found that with increasing accuracy in the first 12 choices the number of lifted cups declined ($\chi^2=18.41$, df=1, $p<0.001$; see Fig. 5*b*). Moreover, subjects lifted fewer cups in the reversal phase compared to the initial phase ($\chi^2=5.78$, df=1, $p=0.016$). There were no other significant effects (all p-values > 0.1).

Discussion

In this experiment, we presented the chimpanzees with a spatial foraging task with very little costs for incorrect choices or unselective search behaviour. Nevertheless and in line with previous findings (Kanngiesser & Call, 2010), the chimpanzees foraged selectively and learnt to discriminate between the cups. In the inhibition task, our results show a signature of a prepotent response. All naïve individuals first chose a clear cup in the first choice of the first session. Moreover, the chimpanzees' performance in the inhibition task was different compared to a discrimination learning task with similar peripheral demands but without the prepotent component. However, despite this initial preference for the clear cups, we found significantly faster learning rates in the inhibition task than the colour discrimination task both within the first session and across sessions. Finally, their search behaviour became more selective and more efficient in that they stopped their search earlier with increasing accuracy within the first 12 choices.

The distractor properties (open/sealed) were manipulated within-subject in the inhibition task but between-subject in the colour discrimination task. One might argue that this difference might have influenced the comparison between the tasks. Note, however, that we neither found a task:distractor condition interaction nor did we find an order effect of distractor condition in the inhibition task. Therefore, we deem it unlikely that the difference in design between the two tasks had a significant effect on the task comparison.Similar to previous 'visible food' interference control studies (Amici et al., 2008; MacLean et al., 2014), the chimpanzees performed very well in the Avoid Visible Food condition despite minimal costs for choosing the incorrect option. The chimpanzees tested in the current study had extensive prior experience with transparent materials. This experience might have contributed to their good performance (e.g, by weakening their prepotent response for the visible but inaccessible food). For example, in many object-choice tasks transparent panels separating the chimpanzees from the human experimenter were used. However, to our knowledge, the chimpanzees did not have direct access to sealed, transparent containers with food items inside before the start of the current study (though we cannot exclude that they have seen transparent containers holding food outside their enclosure). Despite their good performance, we found substantial individual variation in the first session of the Avoid Visible Food condition (range of individual performance: 0.25 – 0.83), which might make this task suitable for psychometric investigation of inhibitory control.

The current findings can be aligned with the associative learning literature. In the Avoid Visible Food condition (with clear, closed distractor cups with inaccessible food items inside), the initial prediction error was large (compared to the Choose Visible Food condition and compared to the colour discrimination). The chimpanzees' preference for the visible (but inaccessible) food led to an unexpected outcome (no food), which might have enabled fast learning consistent with learning models such as the Rescorla-Wagner model (Rescorla & Wagner, 1972). Neuro-cognitive research supports the view that there is a continuum between slow, effortful, executively controlled actions and fast, automatized, and learnt actions (Meier, Lea, & McLaren, 2018; Verbruggen, McLaren, & Chambers, 2014). In the current study, inhibitory control might have played a larger role in the first session; at the same time, the prediction error associated with the initial incorrect choices might have led to faster learning across sessions. Frustration induced by the negative reward prediction error also might have contributed to the fast avoidance of the transparent cup in the Avoid Visible Food condition though the causal relations here remain elusive (i.e., whether frustration and learning were a common effect of the prediction error or whether frustration played a mediating role).

Alternatively, one might argue that the discriminability of the cups might have differed across the tasks. Accordingly, the chimpanzees may have found it easier to discriminate between the transparent and opaque-green cups than between the yellow and blue ones. Due to the chimpanzees' initial preference for the transparent cups and their attempts to open them we deem the prediction error account more likely but we cannot exclude the possibility that the discriminability of the stimuli based on basic perceptual features contributed to the difference between the inhibition and color discrimination task. Moreover, discriminability, unlike the prediction error account, cannot explain the difference between the Avoid Visible Food condition and the Choose Visible Food condition.

In the reversal phase, the subjects adapted slowly to the new task contingencies. One might argue that also in the reversal stage the prediction error is large and therefore learning rates should be high. However in the reversal learning phase, individuals needed to overcome a prepotent response (as in the Avoid Visible Food condition) and they also needed to learn a positive association between a stimulus that served as distractor before and the outcome (the food). This second part might contribute to the slow adjustment in behaviour as compared to the Avoid Visible Food condition. Other factors that have been highlighted in research on reversal learning is the ability to form representations of task space or learning sets and the ability to estimate the likelihood that changes in the task-relevant contingencies can occur (Izquierdo et al., 2017).

The properties of the closed, clear distractor cup in the Avoid Visible Food condition also contributed to the observed differences in learning rates between conditions. The results of the colour discrimination reveal the importance of this factor. Though learning in the colour discrimination task was slower overall, the chimpanzees learnt to discriminate the cups more quickly when the distractor objects were closed cups. Note that the subjects could not see whether distractor cups were closed or open when they entered the room; the difference only became apparent when they turned the cups over. The finding suggests that the chimpanzees' learning rate depended on object knowledge and / or the acquired information concerning the affordances of the open and closed cups. In a comparative framework, the contribution of these factors on species' performance should be considered in the future. Importantly, however, the properties of the distractor (closed or open) can explain the difference between conditions within each task but they do not explain the differences between tasks (inhibition and colour discrimination task), showing the independent contributions of the two manipulations (avoiding visible food, and avoiding sealed cups).

Age was negatively correlated with performance in the first session of the inhibition task and with their perseveration in the inhibition task. Age was also negatively correlated with performance in the colour discrimination task. These findings add to a growing body of research that indicate an age-related decline in performance in task taxing executive control and memory abilities (Lacreuse, Russell, Hopkins, & Herndon, 2014; Manrique & Call, 2015; Völter & Call, 2014).

Experiment 2

The findings of Experiment 1 suggest that a prepotent response and object properties can affect learning rates in a spatial foraging situation. However, previous experience with the materials might have significantly affected individual variation in task performance rather than variation in inhibitory control (e.g., Jelbert et al., 2016). In Experiment 2, we examined if we could set up an inhibition task that did not rely on a previously acquired (and therefore potentially varying) prepotent response but that creates interference during the task. In standard interference control tasks (such as the Stoop task) from the human literature, the interference is created by the nature of the task or context, which either requires the subject to resolve a conflict between cues in order to respond correctly, or does not (see Parrish, Otalora-Garcia, & Beran, 2017, for a similar task interference effect in chimpanzees). We presented the chimpanzees with a similar search task to Experiment 1 in which they were always rewarded with the same food type (pellets). Visible but inaccessible food of two different types (peanuts and pellets) was sealed in the upper part of the cups: one type signalled the presence of food rewards hidden underneath; the other type signalled that the cups did not contain food, and were sealed. In the congruent condition, the to-be-*chosen* food cue matched the reward food type (reach for pellets to get pellets) whereas in the incongruent condition the to-be-*chosen* food cue did not match the reward (reach for peanuts to get pellets). We examined how the increasing expectation to obtain a certain food type created interference and affected the learning rates in the incongruent condition compared to the congruent condition. We hypothesised that the chimpanzees would form expectations about the type of food reward across sessions. This expectation should interfere with the discriminative stimulus in the incongruent condition but not in the congruent condition. Therefore, we expected slower learning rates in the incongruent condition compared to the congruent condition. Previous research provided evidence that a mismatch between food types serving as discriminative stimuli and rewards in a forced-choice paradigm can affect the learning and decision-making in nonhuman primates (Boysen & Berntson, 1995; Schmitt & Fischer, 2011).

Material and methods

Subjects. The same sample of 13 chimpanzees participated in this experiment. Two males were excluded because they threw the cups around as part of their dominance display when entering the test enclosure on three consecutive test days. Our final sample consisted of 7 females and 4 males aged between 8 and 41 years (M_{age} 26.1 years).

Design. Individuals were presented with two conditions, the congruent and incongruent condition, that were blocked into eight consecutive sessions (see Fig. 6). In the incongruent condition, we introduced interference by a mismatch between the food type that the subjects could see in the cylinders and the food type that was actually hidden underneath the cylinders as a reward. In the congruent condition (see Online Resource 4 for a video), the visible food inside the cylinders and the hidden food reward were consistent, i.e. of the same type. We expected that interference caused by the mismatch between visible food items and rewards in the incongruent condition would result in slower learning rates compared to the congruent condition without this mismatch.

The order of the conditions was counterbalanced across subjects. The assignment to the order was pseudo-random with the restriction that both groups were counterbalanced as much as possible for age and sex. Two sessions per testing day were administered for a total of eight testing days.

Setup and materials. We used the same basic set-up as in Experiment 1 except that the cylinders that covered the food rewards were different. In Experiment 2, we presented the chimpanzees with double-cylinders that all consisted of a clear upper part with a visible piece of food inside, either half a banana pellet or a peanut in its shell. This upper part was sealed so that the food items inside the upper part were inaccessible and only served as discriminative stimuli (one type of food signalled the presence of the hidden reward). The lower part of the double-cylinder was opaque (grey). The baited cylinders were open on the bottom, the distractors were sealed on the bottom (a base plate was glued to the inner side of the cylinder). Food items (half banana pellets) served as rewards. We conducted a food preference test with eight of the individuals that took part in the test before we administered Experiment 2. This preference test included pairwise comparisons between pellets, peanuts, and banana chips (with 6 trials per comparisons). We conducted three sessions with six trials per session (two per comparison). The pairwise comparison between pellet and peanut revealed that the chimpanzees chose pellet over peanuts in 63% of trials (median; range: 17 – 100%). The chimpanzees preferred both pellets (median: 100%; range: 67 – 100%) and peanuts (median: 100%; range: 83 – 100%) to banana chips. When examining correlations between the chimpanzees' pellet preference in the preference test and the initial (session 1) or overall performance in Experiment 2, we found no evidence for that food preferences significantly affected the performance in this task (see Table S11). However, our sample was too small to entirely exclude this possibility.

All 24 cylinders (that were distributed in the same manner as in Experiment 1) looked identical except for the food item inside the upper half. In the congruent condition, the 12 cylinders with pellets in the upper half had an open bottom half and were baited with pellets (i.e., the visible food item was consistent with the food type of the hidden reward) whereas the cylinders marked by the peanut in the upper half were the distractor objects with a sealed bottom half. In the incongruent condition, the peanut cylinders had an open bottom half and were baited with pellets (i.e., the visible food item and the food reward were inconsistent) whereas the cylinders with a pellet in the upper half had a sealed bottom half and could not be baited.

Procedure. The procedure was identical to that described for Experiment 1.

Scoring and analysis. Scoring was identical as in Experiment 1. We used a GLMM (GLMM11) with binomial error structure and logit link function (McCullagh & Nelder, 1989) to analyse the first 12 lifted cylinders per session regarding their baiting status (coded as 1 if a baited cylinder was lifted and 0 if an empty cylinder was chosen).Following a significant interaction, we analysed the first four choices per session and condition separately (GLMM 12). We fitted the model in the same manner as GLMM 11 except that the interactions terms including the choice number were removed. The analysis was identical to Experiment 1 with respect to the (maximal) random slope structure, full-null model comparisons using likelihood ratio tests, and model assumption checks.

Results

As predicted, the chimpanzees' performance improved in the congruent condition across sessions but not in the incongruent condition. This difference can be identified particularly in the first choices (lifted cylinders) within each session.

Learning rates (correct choices within the first 12 visited cylinders). We fitted a binomial GLMM (GLMM 11) and included the condition (congruent vs incongruent), session within condition, choice number within session, and all 2 and 3-way interactions between these three predictor variables, age, and sex as test predictors as well as the order of conditions (1 -2) as control predictors. We included the interaction terms with session and choice number because we had observed significant changes in performance both within and between sessions in the inhibition task of Experiment 1. The full model was significant compared to a null model lacking the predictor variables (χ^2=20.85, df=9, *p*=0.013; see Table S12 for a detailed model output). We found a significant 3-way interaction between condition, session, and choice number (χ^2=6.22, df=1, *p*=0.013): in the first sessions there was no difference between the conditions, however, by the 4th testing day (session 7 and 8) individuals performed better in the congruent than incongruent condition particularly in the first choices per session (see Fig. 7). There were no significant effects of age, sex, or order of conditions on task performance (all p-values > 0.1).

Performance in the first four choices per session. Following the significant interaction, we analysed specifically the first four choices per session (GLMM 12; full – null comparison: χ^2=14.98, df=6, *p*=0.020, see Table S13). We found a significant interaction between session and condition (χ^2=6.63, df=1, *p*=0.010): with increasing session number, the apes performed better in the congruent condition compared to the incongruent condition (see Fig. 7). There were no other significant effects on performance (all p-values > 0.1). In line with the results of the GLMM, the chimpanzees performed significantly above chance in the congruent condition on testing day 4 (Wilcoxon signed-rank test: T^+=33.5, N=8, p=0.039) but not on the previous testing days (all p>.1). In the incongruent condition, the chimpanzees' performance did not deviate significantly from chance (all p>.1).

Discussion

The difference in the learning rates between the congruent and incongruent conditions suggests that the mismatch between type of food items they saw in the clear section of the cylinder and food rewards they could retrieve from underneath did induce interference. We detected this interference effect with increasing number of sessions and thus more experience with obtaining the same type of food reward. With increasing number of sessions, the chimpanzees seemed to have formed the expectation to find pellets as rewards, which, in turn, might have triggered the interference effect.

However, this interference effect was apparent only in the first few choices per session. The information the apes gained *within* each session attenuated the effect. Additionally, most of the chimpanzees lifted all cylinders in the area where they were sitting before moving on to another part of the search array. This proximity bias (together with no strong food preferences for pellets over peanuts) likely affected the performance within each session because selectivity for one cup type in the beginning of the session reduced the proportion of this cup type particularly in this part of the search array. For that reason selectivity within their first searches per session can be expected to be highest at the beginning of the session when all cylinders were still in their original position.

A comparable interference effect has recently been reported in the context of a relative quantity judgement task (Parrish, Otalora-Garcia, & Beran, 2017). In this study, the chimpanzees were presented with different containers that had previously been associated with different food rewards and therefore the chimpanzees had acquired preferences for the containers according to their food preferences. When these containers were then used within the relative quantity judgment task, in which the chimpanzees had to remember the position of different food quantities covered by these containers, their container preferences introduced interference. The chimpanzees made more mistakes in incongruent trials in which a preferred container was placed over a small food quantity compared to congruent trials in which a preferred container covered the largest food reward. The interference effect that we found in the current study is different because it is not caused by a previously acquired preference but by the mismatch between the discriminative stimuli and the rewards. Put differently, the interference in the current task seems to be driven by the chimpanzees’ expectation to get what they see.

The current task also parallels the reverse reward contingency paradigm, a 2-option forced-choice paradigm in which the subjects need to select the less preferred option to obtain the preferred option (Boysen et al., 1996; Boysen & Berntson, 1995; Uher & Call, 2008; Vlamings et al., 2006). The chimpanzees (as well as other great ape species) performed poorly in this task though some individuals learnt the reverse contingency (Vlamings et al., 2006). The chimpanzees' performance significantly improved when they could make the discrimination based on Arabic numerals rather than directly based on the food quantities (Boysen et al., 1996; Boysen & Berntson, 1995). Their performance also improved when the food rewards served as discriminative stimulus but were occluded before the apes could choose (Vlamings et al., 2006). In the current task, the chimpanzees also had to cope with a mismatch between discriminative stimulus and the reward. However, in contrast to the reverse reward contingency paradigm, the chimpanzees did not have to choose against a clear food quantity preference. In the reverse reward contingency task the chimpanzees typically had to choose the smaller reward to receive the larger reward. The chimpanzees that participated in the current study did not exhibit a clear-cut preference for pellets over peanuts. Thus, the chimpanzees did not have to choose against a strong pre-existing preference in the incongruent condition. Instead, the increasing expectation to receive pellets as rewards (and not peanuts) induced the interference. In sum, the current task and the reverse reward contingency paradigm share the mismatch between discriminative stimulus and the expected outcome. However, in contrast to the reverse reward contingency paradigm, we introduced this outcome expectation in the course of the experiment and did not rely on a pre-existing preference.

General Discussion

The current study identifies multiple factors contributing to the variation in performance in an inhibition task. These included the accessibility of the food reward, the affordances of the objects serving as hiding places for the food rewards, and the expectation to obtain a certain type of food. Next, we discuss possible mechanisms underpinning these determinants of the chimpanzees' foraging behaviour in this task, and implications for future comparative work.

The chimpanzees took advantage of the object properties of the cylinders, precisely whether the cylinders could function as containers or covers. Importantly, these object properties were not visible at the beginning of the session when the cylinders were all placed in the same orientation with the open side facing to the ground. This functional property became evident only once the chimpanzees turned the cylinders around. This finding can be interpreted in three ways: first, it might be that their discrimination learning was faster because with closed distractor cups the stimuli differed in multiple features (colour and shape) in contrast to the conditions with open distractor cups. Discrimination learning has been found to be faster when primates can use multiple cues to discriminate stimuli (e.g., Warren, 1964). Second, the sealed cylinders might have acquired a negative valence during attempts to open them. The negative valence of the distractor objects might have contributed to faster learning rates. Third, previous experience with a functionally relevant property, the containment function, might have affected the chimpanzees' learning rates. Our sample of zoo-housed chimpanzees had experience with receiving tea or juice from plastic cylinders (of different material, shape, size, and colour as the cylinders used in the current study) during the daily feeding routine. Moreover, they had extensive experience with different cup games with food hidden underneath. From the wild, there is evidence that chimpanzees fold leaves to use them as drinking tools (e.g., Tonooka, 2001). Based on their own prior experience with containers and their behavioural repertoire in the wild it appears plausible that chimpanzees, like human infants (Hespos & Baillargeon, 2006), are sensitive to the containment function of objects. In human infants, expectations about containment develop later than expectations about occlusion alone. Future research will show whether the benefit in learning rates with closed distractor cups is specific to the functionally relevant object property (i.e., the containment function) or whether this merely an example of cue additivity in discrimination learning or the result of failed attempts to open the sealed cylinders.

Additionally, our findings show how the presence of a prepotent response affects learning rates. Inhibition problems are usually associated with an initial failure due to a prepotent action plan that needs to be suppressed (here: reaching for a clear cylinder with food inside without obtaining the food reward). Initial failure might lead to a prediction error which in turn affects learning rates according to some models of associative learning (Rescorla & Wagner, 1972). In line with such an account, the chimpanzees learned faster in conditions with an initial preference for one of the stimuli (the inhibition condition) compared to a condition without such an initial preference (the colour discrimination condition). Neuro-cognitive research with humans and monkeys provided evidence for a common mechanism for detecting response errors, unexpected negative outcomes, or response conflict (in the posterior medial frontal cortex; pMFC) leading to immediate adjustments in behaviour (Kerns et al., 2004; Ridderinkhof et al., 2004). The pMFC-based mechanism that signals a decrease in the probability of obtaining a reward seems to be involved in reinforcement learning in monkeys and humans. In line with this evidence, our results indicate that the prediction error associated with the visible but encased food items led to rapid avoidance learning compared to neutral colour stimuli.

However, previous research suggests that prediction error alone is insufficient to explain the performance in inhibition tasks. In the reverse reward contingency paradigm, the chimpanzees' performance significantly improved when the discriminative cues were not the food rewards themselves but Arabic numerals (Boysen & Berntson, 1995). In other words, the representational format of the discriminative cues influenced the performance in this case. A comparable effect has been found in monkeys (olive baboons and long-tailed macaques; Schmitt & Fischer, 2011).

Additionally, the violation of outcome expectations can lead to opposing effects. In Experiment 1, the chimpanzees quickly learnt to avoid visible but inaccessible food. In Experiment 2, the incongruent pairing of visible encased food stimuli and food rewards led to slower learning rates across sessions. One important difference between the two experiments is that in Experiment 2 the chimpanzees needed to pay attention to the encased food items in the clear cylinders to discriminate stimuli whereas in Experiment 1 they could have just learned to avoid the clear cylinders with increasing experience (and the associated negative feedback).

When using different types of food as rewards or cues in a task, food preferences might affect the performance. In the current study, high food motivation might have made the Avoid Visible Food condition more challenging and the Choose Visible Food condition easier (Experiment 1). Similarly, a preference for pellets over peanuts might have facilitated the congruent condition and exacerbated the incongruent condition (Experiment 2). While the food preferences should not explain the within-subject comparisons in this study, they might have well affected individual differences in performance. Food preferences need to be taken into consideration when applying such tasks to study individual differences.

In summary, the current study demonstrates that, with experience, the chimpanzees show increasing selectivity and efficiency in their spatial foraging behaviour despite minimal costs for unselective search patterns. Their learning rates depended on initial preferences, outcome expectations, and object affordances. When the chimpanzees had a strong initial preference for a certain type of stimuli (i.e., for the visible but encased food items) but these stimuli did not yield rewards, they learnt faster to avoid these stimuli compared to neutral ones (i.e., opaque cylinders of different colours). It is conceivable that the prediction error associated with visible but inaccessible food might have led to faster learning rates despite the initial task interference. The affordances of the objects that served to hide the food rewards also influenced learning rates. In particular, the chimpanzees learnt faster to avoid closed cylinders that could not serve as hiding place for the food raising the possibility that these chimpanzees were sensitive to the containment function of the open cylinders. Finally, increasing experience with a certain type of food reward led to slower learning rates when we introduced a conflict between food that served as discriminative stimulus and as food reward.

We recently argued that comparative research should focus more on identifying signatures of the cognitive ability under investigation in order to establish the content validity of experimental paradigms (Völter et al., 2018). In the current study, we pursued this approach by including another task with identical peripheral demands (the colour discrimination task) but differences in the amount of distractor interference. For species and cohort comparisons potential differences in inhibitory control can only be isolated with appropriate controls (in this case discrimination learning abilities). Additionally, inhibition tasks involving interference that hinges on previous experience of an individual outside the specific experimental context can be problematic in a comparative framework given the vast differences between different captive populations with respect to their environment, husbandry, experimental history, and past experience more generally. Akin to our approach in Experiment 2, we suggest that setting up conflict within an experiment rather than relying on previous experience or existing knowledge may ensure more valid species, cohort, and individual comparisons.

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Table 1

Experiment 1: Overview of tasks and conditions.

Group	**n**	**Initial**		**Reversal**	
		Rewarded cylinders	Distractor cylinders	Rewarded cylinders	Distractor cylinders
Inhibition - Avoid Visible Food (sealed distractor)	7	Green	Visible food (sealed)	Visible food	Green
Inhibition – Choose Visible Food (both open)	6	Visible food	Green	Green	Visible food (sealed)
Colour Discrimination (sealed distractor)	8	A	B (sealed)	B	A (sealed)
Colour Discrimination (both open)	5	A	B	B	A

Note. A and B refer to the colours yellow and blue. The assignment of the colours was counterbalanced across subjects. The same 13 chimpanzees participated in the inhibition and colour discrimination task (order counterbalanced). Within each task, each row refers to another subset of the chimpanzee sample (between-subject manipulation). The group names for the inhibition tasks refer to the initial condition.

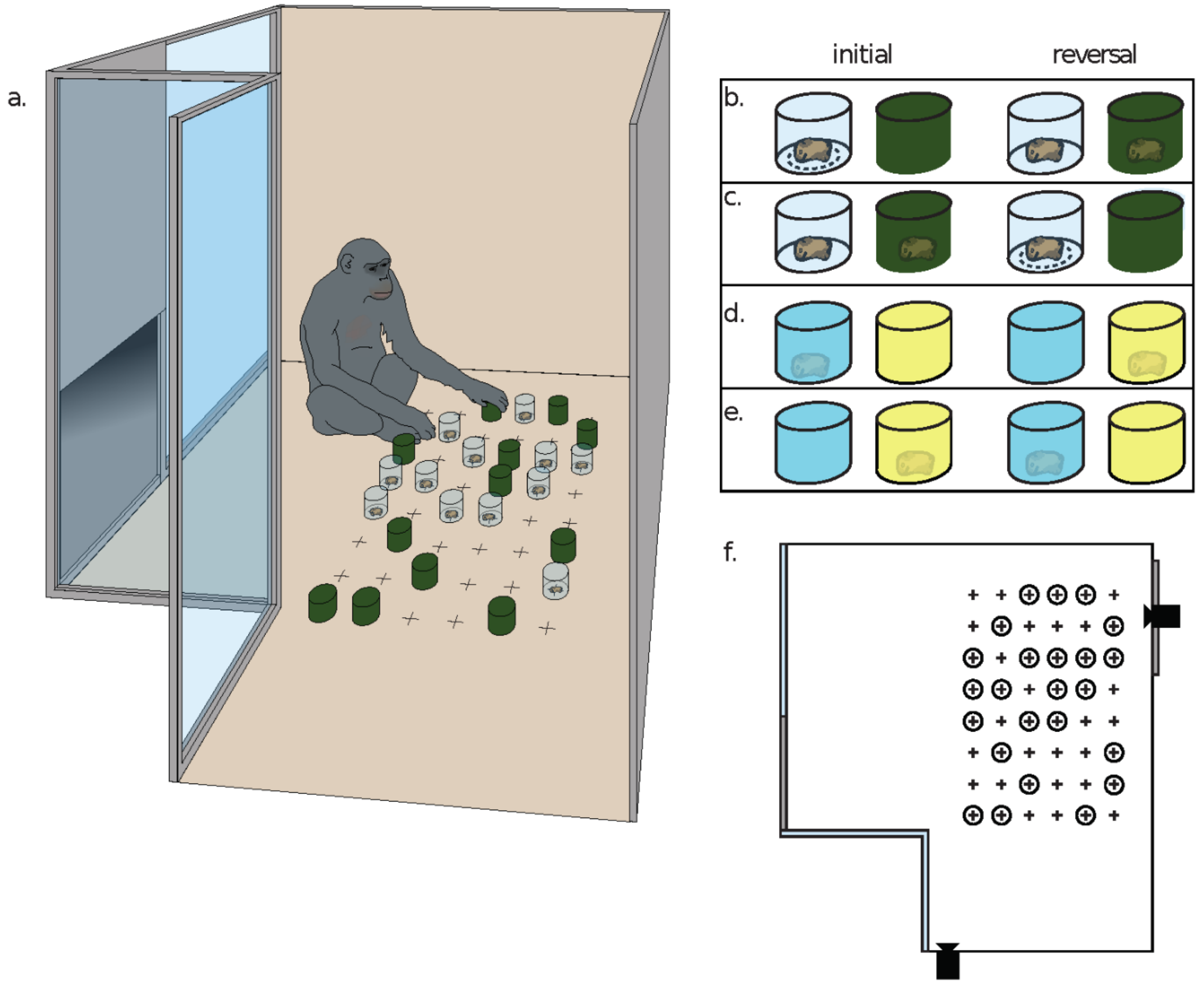

Figure 1. Experiment 1: Illustration of the setup and design. a. overview of the setup; b. in the initial phase *Choose Visible Food* condition (transparent container with accessible food and no food under the opaque cup); in the reversal *Avoid Visible Food* condition (the food inside the transparent cups is inaccessible and food items are hidden under the opaque cups); c. first *Avoid Visible Food* condition then *Choose Visible Food* condition; d. food first under blue (dark grey) cup then under yellow (light grey) cup; e. food first under yellow (light grey) cup then under blue (dark grey) cup; f. birds-eye view of the search array including the camera positions.

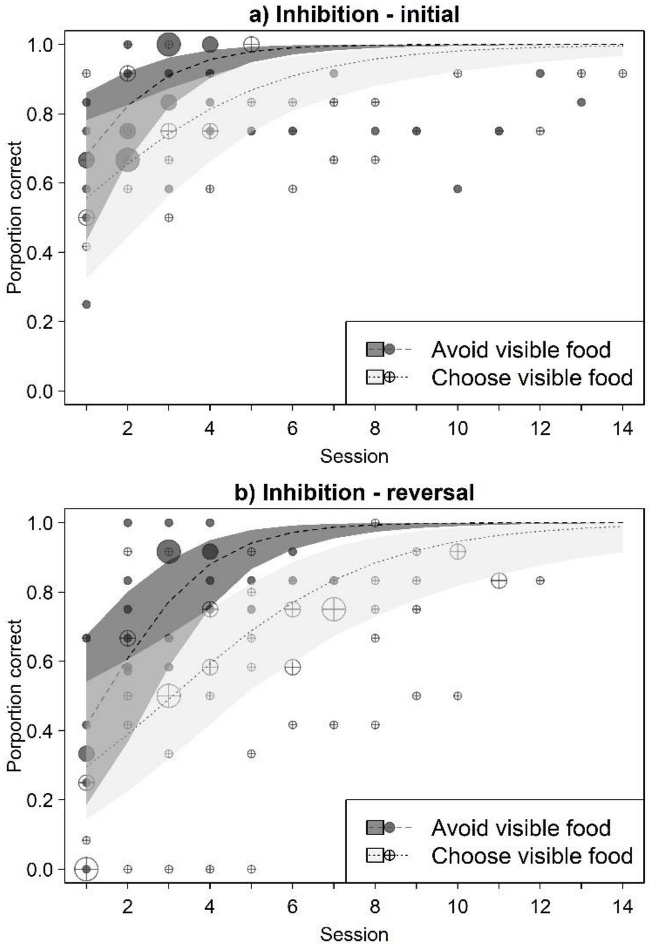

Figure 2. Experiment 1: Inhibition task performance as a function of session and condition (Avoid Visible Food / Choose Visible Food). a) initial learning phase; b) reversal phase. In the Avoid Visible Food condition, the food is hidden under the opaque cup; in the Choose Visible Food condition, the accessible food is inside the clear cup. The dashed / dotted lines show the fitted model for the two conditions and the shaded areas its 95% confidence intervals (with age at its average and sex manually dummy coded and centred). The dots show the proportion of correct choices per session at the individual level. The area of the dots depicts the number of individuals (mean values) per proportion of correct choices and session (N = 1 to 3).

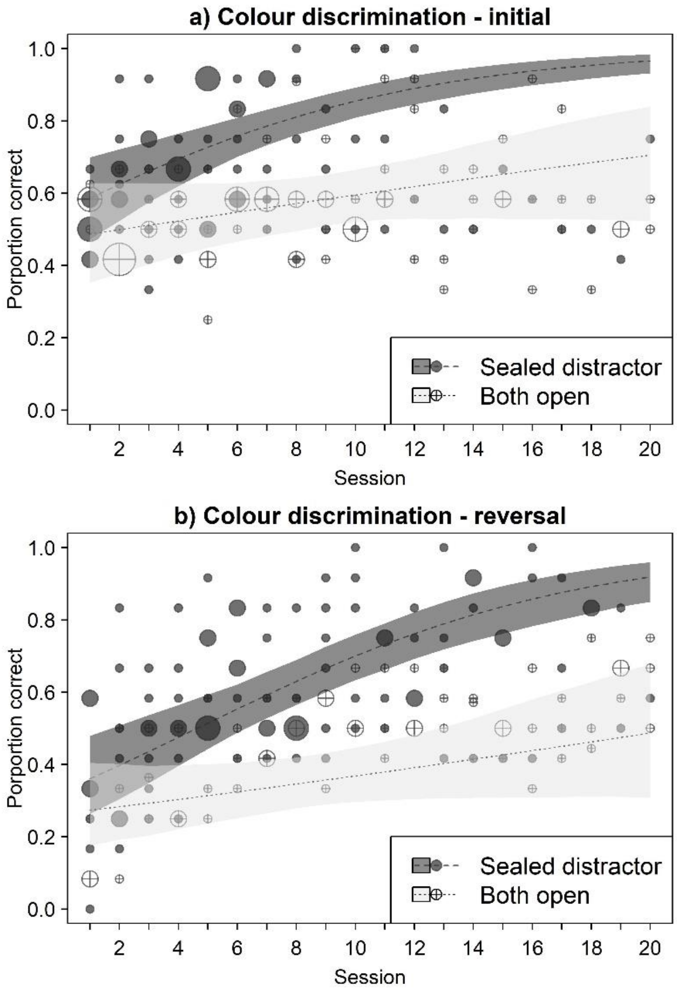

Figure 3. Experiment 1: Colour discrimination performance as a function of session and condition (Sealed distractor / Both Open). a) initial learning phase; b) reversal phase. The dashed / dotted lines show the fitted model for the two distractor conditions and the shaded areas its 95% confidence interval (with age at its average and sex manually dummy coded and centred). The dots show the proportion of correct choices per session at the individual level. The area of the dots depicts the number of individuals per proportion of correct choices and session (N = 1 to 4).

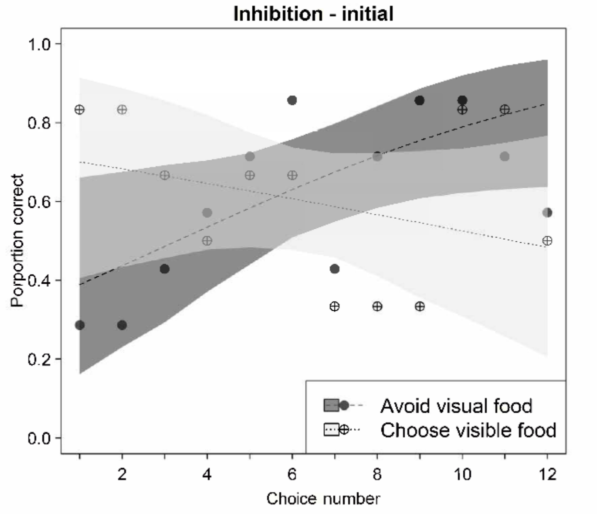

Figure 4. Proportion correct in the first session of the inhibition task (initial phase) as a function of choice number (i.e., the order of lifted cups: 1-12) and the distractor condition. In the Avoid Visual Food condition, the food is hidden under the opaque cup; in the Choose Visible Food, the accessible food is inside the clear cup. The dashed / dotted lines show the model fit for the two distractor conditions and the shaded areas its 95% confidence intervals (with age at its average and sex manually dummy coded and centred). The dots show the mean proportion of correct choices for the two conditions and for each choice. The proportion of correct cups of the remaining, unvisited cups changed within each session as a result of the subjects' choices. We did not correct for the changing probabilities here or in the corresponding analysis.

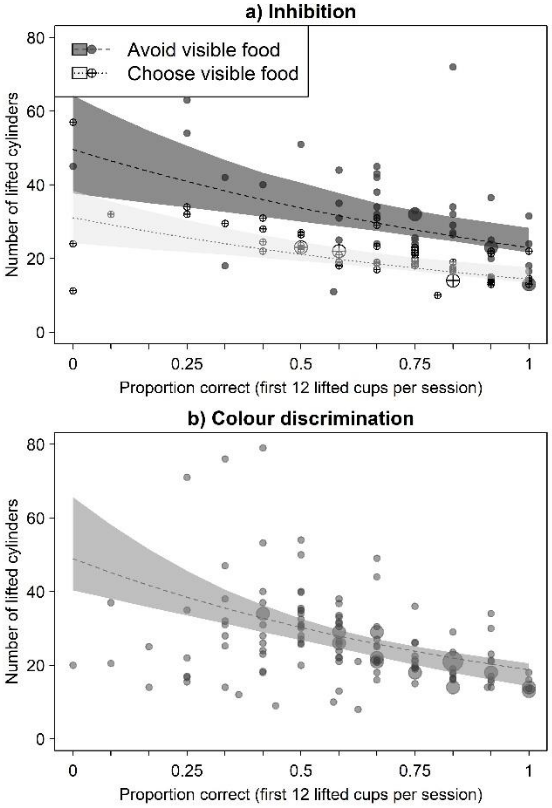

Figure 5. Number of lifted cups per session (including re-visits) as a function of the accuracy within the first 12 lifted cups. a) Inhibition task performance as function of the distractor condition (Avoid Visible Food / Choose Visible Food); b) colour discrimination performance. The dashed / dotted lines show the fitted model for the two distractor conditions (inhibition condition) or for the overall performance (colour discrimination) and the shaded areas its 95% confidence interval (with age at its average and sex manually dummy coded and centred). The dots show the number of lifted cylinders per session at the individual level; the area of the dots represents the number of data points (N = 1 to 4).

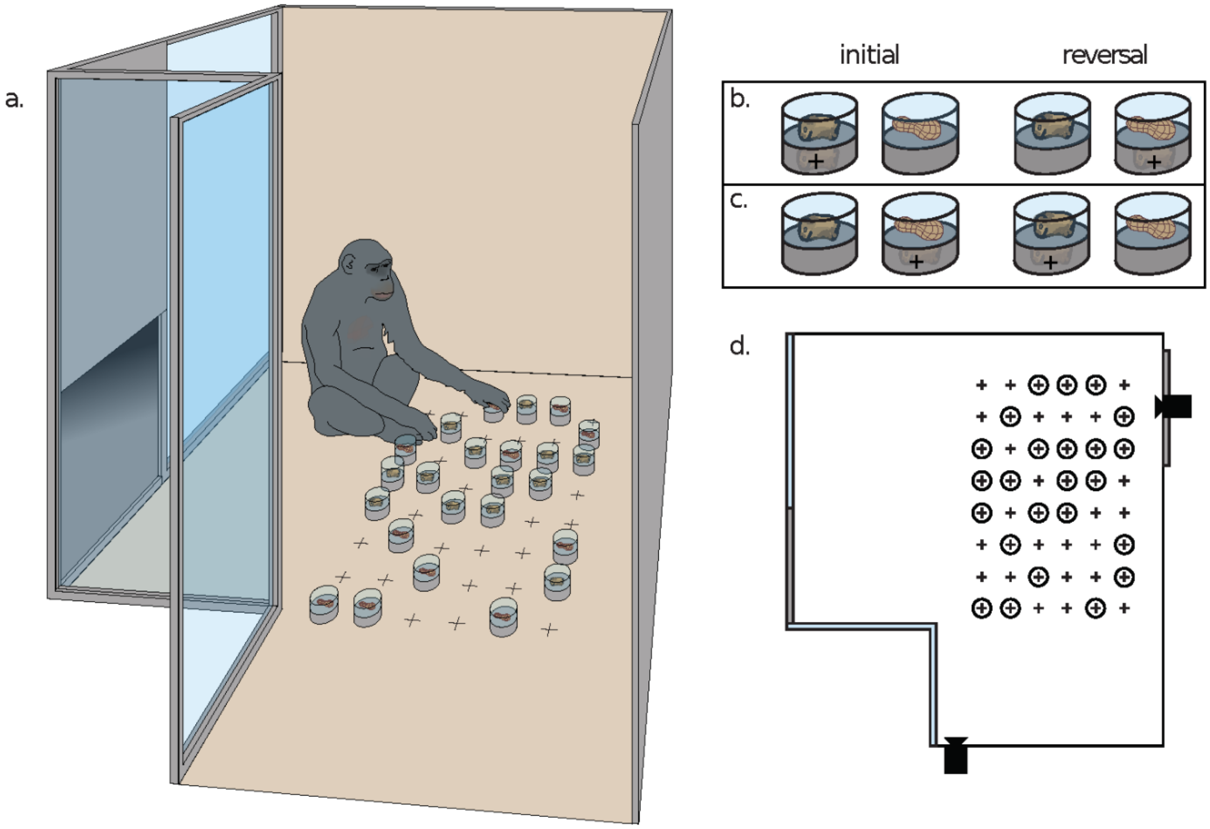

Figure 6. Experiment 2: Illustration of the setup and design. a. overview of the setup; b. congruent condition first group with the pellet hidden under the cylinders marked by a pellet in their upper, clear halves in the initial phase (congruent condition); in the reversal phase, the hidden food rewards were placed under the cylinders marked by a visible peanut (incongruent condition). c. incongruent-first group with the incongruent condition in the initial phase and the congruent condition in the reversal phase; d. birds-eye view of the search array including the camera positions. The plus signs in b. and c. denote the baited cylinders.

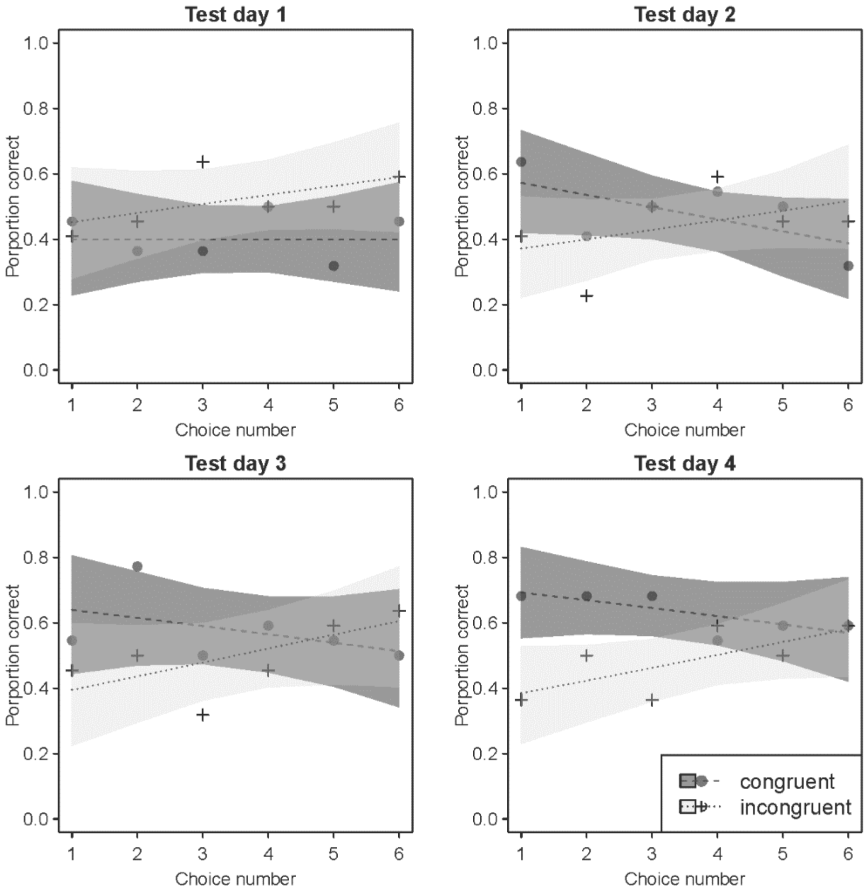

Figure 7. Experiment 2: Task performance (proportion of correct choices) as a function of condition (congruent / incongruent), test day (within each condition; 2 session per test day), and choice number (i.e., the order of lifted cups within condition and session). The dashed / dotted lines show the fitted model for the two conditions and the shaded areas its 95% confidence intervals (with age at its average and sex manually dummy coded and centred). The dots depict average proportion of correct choices per condition, test day, and choice. The proportion of correct cups of the remaining, unvisited cups changed within each session as a result of the subjects' choices. We did not correct for the changing probabilities here or in the corresponding analysis.