The 'Avoid the Empty Cup' Hypothesis Does not Explain Great Apes' (*Gorilla gorilla, Pan paniscus, P. troglodytes, Pongo abelii*) Responses in two 3-Cup 1-Item Inference by Exclusion Tasks

Josep Call[1,2]

[1]School of Psychology and Neuroscience, University of St Andrews, St Andrews, Scotland

[2]Department of Developmental and Comparative Psychology, Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany

Author note

orcid.org/0000-0002-8597-8336

Correspondence concerning this article should be addressed to Josep Call, School of Psychology and Neuroscience, University of St Andrews, St Andrews, Scotland. Email: jc276@st-andrews.ac.uk

Abstract

In the 2-cup 1-item task, subjects are shown a food item which is then hidden inside one of two cups. Several species spontaneously select above chance the baited cup if shown that one of the cups is empty. Although this response may indicate inference by exclusion (if not A, then B), another possibility is that subjects simply avoid choosing the empty cup, not because they expect the food to be in the other cup, but because they know that cup to be empty. I tested whether this hypothesis explains great apes' responses in a 3-cup 1-item task. Subjects saw three opaque cups on a platform with two of them located behind a barrier during baiting. After baiting one of the cups behind the barrier, I revealed the identity of the empty cup that had been located behind the barrier (Experiment 1) or revealed the contents of the center cup (baited in half of the trials), but always removed it before the subjects' choice (Experiment 2). In Experiment 1, subjects preferentially selected the baited cup even though one of the other two cups had not been shown to be empty. In Experiment 2 subjects' preference for the cup that had been located behind the barrier during baiting was modulated by the contents of the removed cup. These results suggest that expectations about the food's location, not just the sight of the empty cup, as postulated by the 'avoid the empty cup' hypothesis, determine apes' responses in the 3-cup 1-item task.

Keywords: inference by exclusion, proto-logic, object permanence, expectations, object search, disjunctive syllogism

The 'Avoid the Empty Cup' Hypothesis Does not Explain Great Apes' (*Gorilla gorilla, Pan paniscus, P. troglodytes, Pongo abelii*) Responses in the 2-Cup 1-Item Inference by Exclusion Task

Understanding the psychological processes guiding animals' responses when confronted with a novel problem that requires an immediate solution is a major undertaking of comparative psychology. Broadly speaking, learning and reasoning are the two main forms of adaptation that have been postulated to explain the emergence and acquisition of novel responses in problem-solving situations (Tolman, 1932; Maier & Schneirla, 1935). A key distinction between them is that learning relies heavily on associative processes while reasoning relies on inferential processes.

Associative processes require co-presence of cues, responses and outcomes (Premack & Premack, 1994). A gradual improvement over time is one of its main signatures, although acquisition can be speeded up when the problem format is presented repeatedly as in learning sets (Harlow, 1949), or when it relies on more specialized forms of learning such imprinting or taste aversion (Sluckin, 1965; Garcia & Koelling, 1966). All other forms of associative learning are thought to be governed by general principles whose main attraction is that they can be applied to a variety of stimuli and responses.

In contrast, inferential processes consist of connecting stimuli and responses despite substantial spatio-temporal gaps between them or combining them to produce novel solutions (Köhler, 1925; Premack & Premack, 1994). This means that inferential processes can produce fully formed responses on the very first trial. In fact, this feature is one of the main signatures used to distinguish learning from reasoning. A point of contention over the years is that inference also requires experience – a fact that some learning theorists have used to attempt to reduce inference to associative processes, effectively equating the kinds of transfer that one sees in associative learning tasks with those observed in inference tasks. Without denying the role that experience plays in inference and problem solving (see Köhler, 1969), it is important not to conflate experience that fuels inferences (often gathered outside the testing situations under different motivational control; see Tolman, 1932) with that obtained while trying to solve the task. More importantly, and leaving theoretical considerations aside, there is ample evidence showing that associative processes fall short of explaining certain responses.

Searching for hidden objects and tracking their invisible displacements is one of the areas that produced some of the most compelling comparative evidence for various forms of inferential reasoning (see Voelter & Call, 2017, for a review). Much of this body of work is grounded on the concept of object permanence (Piaget, 1954), more precisely, on the spatio-temporal properties that determine the very existence of objects and how spatial transformations affect them (e.g., objects persist despite visual occlusion, objects do not continue to exist in their original location after they have moved to another location). An organism capable of using such properties during object search can substantially improve its search efficiency, for instance, by not even trying those responses that are incompatible with the spatio-temporal parameters of the testing setup. In one of the simplest tests of inference by exclusion, the so-called 2-cup, 1-item visual task (henceforth cup task), the experimenter hid a food item inside one of two cups located behind a barrier while apes watched (Call, 2004, see also Grether & Maslow 1937, for a precursor of this task). Upon removal of the barrier, the experimenter showed that one of the cups was empty and allowed the subject to choose between the two cups. Subjects preferentially selected the baited cup. According to an object permanence account, the subjects picked the unopened cup because having seen the food disappear behind the barrier during baiting, and not finding it in the cup opened by the experimenter, they expect to find it in the alternative cup. Its easy implementation and ecological relevance have made this task a popular choice to investigate inference by exclusion in primates (e.g., Call, 2004; De Petrillo & Rosati, 2020; Hill et al., 2011; Marsh et al., 2015; Sabbatini & Visalberghi, 2008; Paukner et al., 2009; Schmidt & Fischer, 2009) and non-primate species including goats, dogs, pigs, elephants, corvids and parrots (Bräuer et al., 2006; Erdőhegyi et al., 2007; Jelbert et al., 2015; Mikolasch et al., 2011, 2012; Nawroth & von Borell, 2015; Nawroth et al., 2014; Pepperberg et al., 2013; Plotnik et al., 2014; Schloegl, 2011; Schloegl et al., 2009; Schloegl et al., 2012; Shaw et al., 2013). Despite its simplicity, the task has revealed substantial inter-individual and inter-specific differences with great apes, monkeys and African grey parrots generally outperforming other species. Moreover, at least for great apes, inter-individual variation in performance on this task seems to be associated with performance on other tasks thought to measure inference (Herrmann & Call, 2012).

However, there is an alternative explanation for selecting the alternative (baited) cup that does not require inference. Instead of expecting the reward in the unopened cup, as predicted by object permanence, subjects might have used a heuristic based on simply avoiding the cup that they *have seen* to be empty without necessarily expecting the food item inside the alternative cup, which is known as the 'avoid the empty cup' hypothesis. As far as I know, this hypothesis was first formulated by Paukner, Anderson and Fujita (2006) in a metacognition study that also tested inferences in capuchin monkeys, and it has been discussed and further elaborated in subsequent work (e.g., Mody and Carey, 2016; Paukner et al., 2009; Penn & Povinelli, 2007; Schmidt & Fischer, 2009). Researchers have proposed heuristics based on particular procedural manipulations as alternative explanations to true object permanence with some regularity (see Jaakkola, 2014, for a review). For instance, choosing the first or the last cup touched by the experimenter has commonly been evaluated as an alternative explanation to true object permanence in sequential invisible displacements (e.g., De Blois et al., 1998; Collier-Baker & Suddendorf, 2006). Although some of these heuristics seem to explain some of the results in some species (e.g., Collier-Baker et al., 2004; Deppe et al., 2009), they do not explain other results (Collier-Baker & Suddendorf, 2006; Pepperberg, 2015; but see Jaakoola, 2015).

Focusing solely on the results of the 2-cup task, the 'avoid the empty cup' hypothesis is entirely viable. Neither the original data, nor those in subsequent studies, can distinguish the 'avoid the cup that has been shown to be empty' from the 'expect the food in the alternative cup' hypotheses. However, three pieces of indirect evidence suggest that merely avoiding the empty cup without forming expectations about the contents of the alternative cup might not be entirely plausible, at least for some species. First, dogs, apes, parrots and macaques encode not just the location but also the type of item that is hidden in that location (Braeuer & Call, 2011; Mendes et al., 2008; 2011; Pepperberg et al., 1997, 2013; Phillips & Santos, 2007; Tinklepaugh, 1928, 1932). More specifically, subjects search more often and/or longer the original container if what they recover is different from what they observed being deposited in that container, suggesting that they had formed an expectation about the container's contents. Second, apes and parrots can find an item above chance levels after multiple stage 6 invisible displacements involving three cups, even though some cups are not visited and crucially, none of the cups are shown to be empty (e.g., Collier-Baker & Suddendorf, 2006; de Blois et al., 1998; Pepperberg et al., 1997). This makes the use of the 'avoid the empty cup' heuristic moot (see Schmidt & Fischer, 2009). Third, apes and African grey parrots have passed the most complex forms of inference that require encoding both the type of item and the location where it is placed (Call, 2006; Pepperberg et al., 2013; Premack & Premack, 1994). For instance, if subjects see a grape go under cup A and a banana under cup B, and behind a screen the experimenter removes the banana and discards it while the subject watches, subjects pick the cup holding the grape even though they have not seen the experimenter remove the banana from one of the cups. Here again, the subjects do not see any empty cup, just two upside down cups on a platform and they have to infer which one is still baited. Moreover, control conditions show that subjects do not solve this task by learning a conditional discrimination (Call, 2006; Pepperberg et al., 2013).

But indirect evidence, no matter how suggestive, is insufficient to conclusively refute the 'avoid the empty cup' hypothesis. Paukner et al. (2009) formally tested this hypothesis by presenting capuchin monkeys with three opaque cups, but before they could choose one of them, they showed the monkeys that one cup was empty. The other two cups were baited but monkeys did not know because they had neither witnessed the baiting nor seen the contents of the baited cups. Paukner et al. (2009) found that monkeys did indeed avoid the empty cup under such conditions -a finding that they interpreted as evidence that avoiding the empty could explain monkeys' performance in the inferential cup task that they also administered. However, Paukner's et al. (2009) test is not diagnostic of inference because monkeys were never shown that food might be hidden in any of the cups, and consequently, they might or might not have formed an expectation about food being inside one of the cups. Without this expectation (which was also missing in Grether and Maslow, 1937), this is not a test of inference, it is a test of memory which shows that monkeys remember that the empty cup is indeed empty. In other words, although avoiding the empty cup in the cup task does not necessarily constitute evidence of inference, avoiding the empty when no expectation has been formed does not constitute evidence for a lack of inference either.

My goal in this study is to directly test the idea that all that apes are doing in the cup task is to avoid the empty cup without forming an expectation about the contents of the other cup. To this end, I conducted two experiments grounded on the concept of object permanence, with expectations about food location playing a key role. Subjects faced three opaque cups on a platform with two of them located behind a barrier. The experimenter showed a food item to the subject and baited one of the two cups behind the barrier. Thus, the subject knew that food had disappeared behind the barrier but did not know under which cup it had been placed. After removing the barrier, the experimenter showed the contents of one of the cups that had been located behind the barrier. In Experiment 1, this cup was always empty and then subjects had to choose between three cups: the cup that had just been shown to be empty and two other cups, one that had been behind the barrier during baiting and one that had not. Unlike previous studies, this experiment offered two alternatives to the lifted (empty) cup, instead of just one, thus testing whether subjects showed a preference for the cup that was behind the barrier when baiting took place, a prediction that the 'avoid the empty cup' hypothesis does not make. In Experiment 2, the lifted cup was baited in half of the trials but it was always removed from the platform (including its contents if baited) before subject could choose between the two remaining cups. In other words, this experiment tested whether the preference for the cup that had been located behind the barrier during baiting was modulated by the contents of the removed cup, once again, a prediction that the 'avoid the empty cup' hypothesis does not make. To test the idea that inference rather than learning some heuristic was responsible for the subjects' responses, I also tested whether subjects were capable of solving the task based on observable heuristics (such as the experimenter touching some cups but not others prior to the subject's choice) rather than object knowledge.

Experiment 1

The 'avoid the empty cup' hypothesis postulates that subjects in inference by exclusion tasks with one alternative besides the empty cup, choose the baited container, not because they expect it to be baited but because they are avoiding the empty cup. The experimental condition in the current task, offered not one, but two alternative cups to the empty cup. The only difference between the two alternatives is that one of them was placed behind the barrier (next to the empty cup) when the baiting took place. Based on object permanence, I predicted that subjects would show a preference for the alternative cup that had been behind the barrier, a result that the ‘avoid the empty cup’ hypothesis does not predict. If subjects expected that the food that they saw move behind the barrier (but that they never saw go into any of the two cups) should still be there, I predicted that they would select the cup that was behind the barrier when the baiting took place.

The control condition in this experiment was designed to check whether subjects’ responses were based on experimenter-given cues or the use of a heuristic based on the presence of the barrier and touching (or not touching one of the alternative cups). Crucially, the control condition was solvable by combining two heuristics: pick the cup that was behind the barrier *and* was touched before the choice. I chose these cues because they are the kinds of cues that are often invoked as alternatives to object knowledge in object permanence tasks including the current experimental condition. Subjects could learn to use these cues over trials, or if they had some pre-existing preference for them, use them starting on trial 1. If subjects used those arbitrary cues (or any other? experimenter-given cues) to find the food, they should be equally successful in the experimental and control conditions.

Method

Subjects

Twenty-three great apes housed at the Wolfgang Köhler Research Center in Leipzig Zoo (Germany) participated in the study (see Table 1). They included six bonobos (*Pan paniscus*), six chimpanzees (*Pan troglodytes*), four gorillas (*Gorilla gorilla*) and seven orangutans (*Pongo abelii*). There were 17 females and six males ranging from 5 to 36 years of age (M = 16.2, SD=8.6). Seven subjects were nursery-reared, 14 mother-reared and two (the oldest ones) had unknown rearing histories. All subjects lived in social groups of various sizes with access to indoor and outdoor areas that included natural vegetation, trees and other climbing structures to increase vertical space. Subjects were individually tested between July 2009 and April 2010 in their indoor cages and they were not food- or water-deprived. Research protocols strictly adhered to the legal requirements of Germany and it was approved by the ethics committee of the Max Planck Institute for Evolutionary

Anthropology and the Leipzig Zoo. I followed all applicable international, national and institutional guidelines concerning behavioral (i.e., non-invasive) research with nonhuman primates.

Table 1

Materials

The apparatus consisted of a sliding platform (80 cm x 40 cm) mounted on a frame attached to the cage mesh. Three identical blue opaque cylindrical flower pots (10 cm in diameter x 12 cm in height) and three white paper cup bases (5 cm in diameter x 2 cm in height) were placed on the sliding platform. The paper cup bases could hold a highly preferred food item (banana slice or pellet) and they were covered by the blue cups. The combination of cup and paper cup was used to minimize the possibility that subjects might be able to see the food under the blue cups if no paper bases were present. A cardboard barrier (50 cm x 30 cm) placed in front of the cups allowed the experimenter to bait the cups outside of the subject's view. The three cups on the platform were aligned and each occupied the left, center and right side positions on the platform flush against the platform's front edge farthest away from the experimenter. When the barrier was placed on the left side of the platform, it blocked the subject's view of the left and center cups while when placed on the right side, it blocked the subject's view of the right and center cups (see Figure 1).

Procedure

Subjects were tested individually in their testing or sleeping rooms. They received one experimental session and one control session. In the experimental condition the experimenter sat behind the platform facing the subject. He placed the three paper cup bases on the platform and covered them with the blue cups in an upside down position. Then he placed the barrier on the platform between the cups and the subject, either on the left side (blocking the left and center cups) or the right side (blocking the center and right cups). The experimenter then showed a food item to the subject and hid it under one of the two cups behind the barrier. The experimenter always lifted both cups (left to right) behind the barrier and deposited the food item under one of them. Upon completing the baiting, the experimenter removed the barrier and lifted the empty cup that was behind the barrier. In half of the trials this meant that the center cup was lifted and in the other half the side cup was lifted. After making sure that the subject saw that the lifted cup was empty, the experimenter placed it back in its original position. The control condition was identical to the experimental condition except that the experimenter did not lift the empty cup. Then the experimenter closed his eyes when he pushed the platform forward and opened his eyes as soon as the platform hit the mesh. By that time, subjects had typically already selected one of the cups. If they had not, the experimenter continued to face forward and down until the subject made a choice. I considered a choice as the first cup the subject touched or pointed to. If subjects pointed to the baited cup, they received its contents but if they pointed to one of the empty cups they received nothing.

Figure 1

In half of the trials of the experimental and control conditions (touch trials), the experimenter placed each of his hands simultaneously on the baited cup and the empty cup that had been outside the barrier during baiting and removed them after 2-3 seconds right before pushing the platform forward. This manipulation allowed for testing the use of combined heuristics and ensured that the subjects' attention had been drawn to all three cups at some point during the presentation. In the other half of the trials (non-touch trials), the experimenter did not touch any of the cups before pushing the platform forward. Non-touch trials are the usual way to present the 2-cup 1-item task and they served to assess whether subjects would preferentially select those cups that had been behind the barrier during baiting (in the absence of touching) and crucially, they served to assess the effect of the experimenter touching two of the cups before letting subjects choose.

Subjects received one experimental and one control session in that order separated by at least one day (range 1-11 days). I did not counterbalance the order of the sessions to be able to test all subjects with the inference condition first, without any potential carry over from the control condition. Each session consisted of 12 trials, six touch and six non-touch, presented in blocks of six consecutive trials within the session and counterbalanced across subjects. Additionally, the experimenter counterbalanced within a session whether 1) the barrier was placed on the left or right side and 2) the baited cup was center or side. Within a session, the food item never appeared in the same position for more than two consecutive trials.

Data coding and analysis

All trials were videotaped and scored in real time on a coding sheet. The dependent variable was the cup selected by the subject. Inter-observer reliability on the dependent variable based on 26% of the trials coded by an independent observer was excellent (kappa=0.979, N=144). I analysed whether the subjects' choices varied as a function of condition (experimental, control) and touching the non-lifted cups before the subjects' choice (yes/no) and the position of the baited cup (center / side). When the baited cup ended up in the center location, two cups whose contents had not been revealed were adjacent (the lifted cup invariably appeared on one of the sides). In contrast, when the baited cup ended up in one of the side locations, two cups whose contents had not been revealed were non-adjacent (the lifted cup invariably appeared on the center location).

I used a Generalized Estimating Equations (GEE) with binomial error structure and logit link function to test the effect of Species (bonobo, chimpanzee, gorilla, orang-utan), Condition (experimental, control), Touched cups before choice (yes, no), Baited location (center, side) and Trial number on the trial-by-trial choices directed at the baited cup. I entered trial number as co-variate, the rest of the factors as fixed effects and subject ID as the subject variable. I checked the model's fit by comparing the Quasilikelihood under the Independence model Criterion (QIC) of the full model with a model without the factors and their interactions included. The full model including all factors and interactions failed to satisfy the convergence criteria. Consequently, I used a reduced model that included the main effects and the 2-way interactions between the fixed factors and compared its fit with a model without including those factors and interactions. Removal of the baited location factor would have allowed me to run a full model but it was deemed more important to include this factor in a reduced model than omit it from the analysis.

I also conducted a GEE with the same structure, function, and factors as the previous model to analyse their effect on the types of errors committed by subjects. Subjects could err by either selecting the empty cup that had been behind the barrier during baiting or the cup that had been in the open during the baiting (and was therefore empty). I used a binomial test to assess performance at the individual level. Subjects selected the baited cup above chance levels (expected P=0.33) if they chose it in at least eight of the 12 trials. I conducted all analyses in SPSS v. 26 using the commands Generalized Estimating Equations and non parametric statistics to run the GEEs and binomial tests, respectively.

Unless otherwise indicated, I used two-tailed statistics for all analyses except for those with directional predictions. Namely, based on the object permanence literature I predicted that subjects would prefer the cups that had been behind the barrier during baiting in both conditions. Additionally, I predicted that subjects would select the baited cup more often in the experimental than the control condition. However, if subjects solved the problem by combining heuristics, they would perform equally well in both conditions.

Results

Individual analyses revealed that 19 apes selected the baited cup above chance levels in the experimental condition (Binomial test: P<0.02, 1-tailed) whereas only four did so in the control condition (see Table 1). Focusing exclusively on the first trial revealed that subjects were above chance in the experimental condition (14/23, Binomial test: P=0.012) but not in the control condition (9/23, Binomial test: P=0.68).

The GEE model that included the main effects and 2-way interactions fit the data on the likelihood of selecting the baited cup better than a model without them, *QIC*: 689.40 vs. *QIC*: 726.61, N=552, Table 2. Re-running the model after eliminating the non-significant terms confirmed this results and produced a slightly better fitting model, *QIC*: 686.21, N=552. Subjects performed significantly better in the experimental than control condition, χ^2=31.38, df=1, $p < .001$, 1-tailed.

Additionally, touching the cups significantly reduced performance, χ^2=8.69, df=1, $p < 0.003$. However, these results need to be interpreted with caution because there were also significant interactions between Species and Condition, χ^2=8.01, df=3, $p = 0.046$, and Species by Touched cup, χ^2= 12.17, df=3, p =0.007.

Table 2

Figure 2 presents the likelihood of subjects selecting the baited cup as a function of species and condition. All species except bonobos, χ^2= 0.432, df=1, $p = 0.51$, selected the baited cup significantly more often in the experimental than the control condition, chimpanzees: χ^2=7.53, df=1, $p = 0.006$; gorillas: χ^2=19.09, df=1, $p < 0.001$; orangutans: χ^2=16.21, df=1, $p < 0.001$.

Figure 2

Figure 3 presents the likelihood of subjects selecting the baited cup as a function of species and touch. Gorillas performed significantly worse when the experimenter touched the cups prior to their selection, χ^2= 15.73, df=1, $p < 0.001$. In contrast, the other species performed equally regardless of the experimenter touching the cups, bonobos: χ^2=0.35, df=1, $p = 0.56$; chimpanzees: χ^2=0.03, df=1, $p = 0.86$; orangutans: χ^2=1.11, df=1, $p = 0.29$).

Figure 3

A model investigating the types of errors as a function of the factors included in the previous model provided a better fit than a model without those factors, *QIC*=233.13 vs *QIC*=259.80, N=200, see Table 3. Re-running the model after eliminating the non-significant terms confirmed this result and produced a better fit, *QIC*: 206.93, N=200. Subjects were significantly more likely to select the empty cup that had been outside the barrier during baiting in the experimental than the control condition, χ^2=16.83, df=1, $p < 0.001$. Although the factor Baited location was no longer significant in this later model, χ^2=2.98, df=1, $p = 0.084$, see Table 3, the significant interaction between Condition and Baited location persisted, χ^2=4.32, df=1, $p = 0.038$.

Table 3

Figure 4 presents the likelihood of subjects selecting the cup that had been located outside the barrier during baiting as a function of Condition and Baited location. In the experimental condition, subjects were significantly more likely to select this cup when the baited cup occupied the central as opposed to a side position, χ^2= 8.99, df=1, $p = 0.003$. In other words, when the two empty cups occupied the two side positions, subjects were more likely to select the cup that had been located outside the barrier during baiting compared to when the two empty cups occupied adjacent positions. In contrast, in the control condition there were no significant differences in the likelihood of selecting the cup that had been located outside the barrier during baiting as a function of the location of the baited cup, χ^2=0.03, df=1, $p = 0.86$.

Figure 4

Discussion

Upon seeing that one of the three available cups was empty, subjects showed a preference for the cup that had been located behind the barrier during the baiting as opposed to the cup left in the open. Crucially, chimpanzees, gorillas and orang-utans, unlike bonobos, selected the baited cup more often in the experimental than the control condition. The preference for the baited cup in the experimental condition was already apparent in the first trial. Subjects' preferences occurred regardless of whether the experimenter touched both cups or not at the time choice. However, gorillas, unlike the other species, were less likely to select the baited cup when the experimenter touched the two cups that had not been lifted before subjects made a choice. The error analyses (choosing the empty cup) revealed that when subjects had not seen any empty cup (control condition), they preferentially erred by choosing the empty cup that had been located behind the barrier during baiting, but they shifted their preference towards the cup that had been in the open during baiting in the experimental condition, especially if the two empty cups occupied the two side positions on the platform. Their preferences for the baited and empty cups remained unchanged over trials.

The 'avoid-the-empty-cup' hypothesis alone cannot explain the preference for the baited cup over the cup that remained in the open during baiting because this hypothesis predicts no preference for one of the non-lifted cups. Furthermore, a preference for the cup that was located behind the barrier during baiting alone is also insufficient to explain the current results because it does not predict that subjects should perform better in the experimental than the control condition.

Having ruled out the use of single heuristics (avoid empty cup, choose hidden cup), one possibility is that individuals succeeded in the experimental condition because they combined these two heuristics: pick the cup that was behind the barrier during baiting that remained untouched by the experimenter after the removal of the barrier. If this were the case, they should have also selected the baited cup at similar levels in the control condition because this combination was deterministic, but they did not do so. Incidentally, focusing on the touched as opposed to the untouched cup could have produced the same positive result as in the control condition, but once again, subjects failed to do so.

Apes' failure to distinguish between the two cups that had been located behind the barrier in the control condition is particularly revealing because this condition was always conducted after the experimental condition, precisely to check if they had succeeded in the latter by using this heuristic. If they had used it, they should have continued to perform well in at least one of the touch / no touch manipulations before the subjects' choice. But they did not. Furthermore, it is unlikely that their failure to use this combined heuristic was caused by the weak nature of the cues presented. First, their preference for the cups located behind the barrier during baiting proved that they did pay attention to which cup was located behind the barrier during baiting. Second, touching stimuli (and the order in which this occurs) is one of the main cues invoked (and tested) as an alternative explanation to inferential reasoning and object permanence (e.g., Neiworth et al., 2003; Collier-Baker & Suddendorf, 2006). In fact, gorillas were affected by the experimenter touching the cups prior to their choice, and still they performed significantly better in the experimental than the control condition.

A revised version of the ‘avoid the empty cup’ hypothesis based on paying attention to the general location of food (e.g., the two cups behind the barrier) and then avoiding the empty cup could also explain the results. However, one would have to make the assumption that apes completely ignored the cup that was in the open during baiting. The results show that this was not the case because they chose it in 12% of the total trials (67/552; experimental=45/276; control=22/276). More importantly, I highlighted that cup in touch trials, precisely to make sure that they paid attention to it, and the results did not change even though the data showed that they paid attention. Note that although gorillas were affected by the experimenter touching the cups prior to their choice, this effect occurred in both the experimental and control condition, and it decreased rather than increased their performance. Thus, touching the cups may have attracted attention to the cup that had been in the open during baiting, thus reducing their choices towards the other touched (and baited) cup.

There is another piece of evidence that indicated that the preference for the baited cup was not solely determined by seeing the alternative empty. Subjects also preferred the cups that had been located behind the barrier during baiting in the control condition where no cup was shown to be empty. This is consistent with the data from numerous studies on object permanence and object individuation (see Cacchione & Rakoczy, 2017) and it suggests that subjects had already formed an expectation about the potential food location, thus reinforcing the idea that expectations are a key component of their inferential processes. Indeed, most of the errors in the control condition occurred when subjects selected the empty cup that had been behind the barrier during baiting. In contrast, most of the errors in the experimental condition occurred when subjects selected the empty cup that had been outside the barrier during baiting, which is not surprising because they had just seen the other empty cup. Subjects' likelihood to err by choosing the empty cup that had been outside the barrier during baiting in the experimental condition was particularly pronounced when the baited cup occupied the central position in the array. There are at least two explanations for this finding. One possibility is that they made a retrieval error since it is known that primates' encoding/retrieval accuracy is poorer for the internal compared to external containers in an array (Beran et al., 2005; Hribar & Call, 2011; Kubo-Kawai & Kawai, 2007). Another possibility is that subjects had a priori postulated where the food would be located and when it was not there, they expanded their search to include the other cups. In other words, they may have not conceived that if the food was not under one of the cups that was located behind the barrier during baiting, it should be under the other. Future studies are needed to empirically test these possibilities. Additionally, it is unlikely that this preference merely reflects an attentional effect – the baited cup actually disappeared behind a barrier during baiting, subjects never saw it being baited and as I noted earlier, highlighting two cups in touch trials before their choice did not change the outcome except for gorillas.

All species preferentially selected the baited cup in the experimental compared to the control condition except bonobos. This outcome was unexpected because previous studies had found no differences between bonobos and other species in several inferential reasoning tasks, or more broadly, object concept tasks (e.g., Barth & Call, 2006; Call, 2004, 2006; Mendes et al., 2008). One possibility is that this difference reflects individual differences rather than species differences. The larger response variability detected in the bonobo sample seems to support this idea. Another possibility is that more powerful statistical techniques used here (GLMM or GEE) are more suitable for detecting even small inter-specific differences, compared to more traditional techniques. Future studies should investigate this aspect in greater detail.

Approximately 12% of the total choices were directed at the cup that had been outside the barrier during baiting, especially in the experimental condition where subjects selected this cup about twice as often than in the control condition (45 vs 22). Moreover, subjects were more likely to select it when the two empty cups occupied the side positions in the platform (and the baited cup was in the center position). One possible explanation for this finding is that cups located in interior positions are less memorable than those occupying more external locations (closer to the platform's edge). Indeed, primates may remember better those locations closer to the edge of the platform or make more accurate selections when multiple baited locations are adjacent rather than non-adjacent (e.g., Beran et al., 2005; Hribar & Call, 2011).

In sum, explanations based on heuristics about simply avoiding the empty cup or choosing those cups where the reward disappeared fall short of fully explaining the data. A key missing aspect in those explanations is the role that the contents of the lifted cup and the subsequent expectations that it generates regarding the contents of the remaining unlifted cups. In the next experiment, I tested the importance of this aspect using a modified version of the current task in which subjects sometimes were able to see, but never choose, the contents of the lifted cup.

Experiment 2

In this experiment, just like in Experiment 1, subjects faced three cups on a platform with food hidden under one of them while the barrier blocked two of the cups (either left+center, or center+right). In the experimental condition, I revealed the contents of the center cup (baited in half of the trials) and removed this cup from the platform (including its content). The control condition was identical to the experimental condition except that I did not reveal the contents of the center cup prior to its removal. Based on the results of Experiment 1, I predicted that subjects would show a preference for cups that had been located behind the barrier during baiting. Crucially, if they used their expectations about the food location to solve the task, I predicted that subjects would decrease their preference for the hidden cup when they saw that the removed cup was baited (and therefore the food gone). Conversely, they would increase their preference for the hidden cup when they saw that the removed cup was empty (and therefore the food was still there). This would indicate that knowing about the contents of the lifted cup modulated their preference for the remaining cup that had been located behind the barrier during baiting.

Method

Subjects

Twenty-three great apes participated in the study (see Table 4). They included four bonobos (*Pan paniscus*), 12 chimpanzees (*Pan troglodytes*), and seven orangutans (*Pongo abelii*) with ages ranging from 5 to 49 years (M = 19.7, SD=12.0). Subjects were tested between December 2014 and December 2015. Two bonobos, three chimpanzees and five orang-utans had also participated in Experiment 1. As in the previous experiment, research strictly adhered to the legal requirements of Germany and it was approved by the ethics committee of the Max Planck Institute for Evolutionary Anthropology and the Leipzig Zoo.

Table 4

Materials

The apparatus was the same as in the previous experiment except that the blue cups were replaced with three identical black opaque bowls (9 cm in diameter x 10 cm in height) and the cardboard barrier was replaced by a grey plastic barrier of the same size.

Procedure

The procedure was the same as in Experiment 1 except that the experimenter always showed the subject that all cups were empty (except for the food holder) at the beginning of the trial (see Figure 5). This is a practice that is used in some studies but not others. In addition, after the baiting was completed, the experimenter only manipulated the center cup and *always* removed it from the platform before the subject could choose. Prior to its removal, however, he showed its contents to the subject by lifting it in half of the trials (experimental condition: contents shown). In the other half of the trials (control condition: contents not shown), the experimenter removed the cup but did not show its contents to the subject. Since the position of the food item was fully counterbalanced across trials, this resulted in half of the experimental trials revealing an empty cup (Contents type: empty) and the other half a baited cup (Contents type: baited). Similarly, in half of the control trials the cup was empty and in the other half it was baited. These manipulations created four types of trials: Experimental (baited), Experimental (empty), Control (baited) Control (empty). Following the removal of the center cup, the experimenter closed his eyes and pushed the platform forward for the subject to choose between the two remaining cups.

Figure 5

Subjects received three 16-trial sessions administered 1 to 6 days apart. Each session consisted of 4 trials of each of the four types mentioned earlier, two with the barrier placed on the left side and two with the barrier on the right side. Within a session food appeared 8 times in the center and 8 times in the sides (4 left, 4 right), respectively. The order of presentation of the trials was pseudorandomized with the constraint that it could not appear more than three times under the same cup on consecutive trials.

Data coding and analysis

I used the same basic scoring procedure as in Experiment 1. The dependent variable was the proportion of trials in which subject selected the cup that had been located behind the barrier during baiting. One subject (Jeudi) failed to respond in trial 41 resulting in 1103 valid trials. Inter-observer reliability on the dependent variable based on 22% of the trials coded by an independent observer was excellent (kappa=0.983, N=240). Note that unlike Experiment 1, the food in Experiment 2 was still in one of the cups in only half of the trials. I analysed whether the subjects' choices varied as a function of the contents of the removed cup (Contents type: baited empty) and whether this contents was shown to the subject (Contents shown: shown, not shown).

I also used the same statistical analysis as in Experiment 1. More specifically, I used the same kind of GEE that I used in Experiment 1 to analyse the effect of Contents shown, Contents type, and Species on the likelihood of selected the cup that had been located behind the barrier during baiting. I used Binomial tests to assess subjects' individual performance, including their first trial performance in each of the conditions. Subjects selected the cup that had been behind the barrier during baiting cup above chance levels (expected P=0.50) if they chose it in at least 10 of the 12 trials. Unless otherwise indicated, I used two-tailed statistics for all analyses except for those with directional predictions. Namely, based on the object permanence literature I predicted that subjects would be less likely to select the cup that had been behind the barrier if they saw that the removed cup contained the food (=there is no food left on the platform) compared to when they did not see it. Conversely, I predicted that subjects would be more likely to select the cup that had been behind the barrier if they saw that the removed cup contained no food (=there is still food left on the platform) compared to when they did not see it.

Results

Individual analyses considering all trials revealed that five subjects (out of 23) selected above chance levels (Binomial test: $p < 0.02$ 1-tailed) the cup that had been located behind the barrier during baiting when they saw that the removed cup was baited whereas 17 subjects (out of 23) did so when they saw that the removed cup was empty (see Table 4). In contrast, when the contents of the removed cup was not shown (control condition), 14 and 12 subjects selected above chance levels (Binomial test: $p < 0.02$ 1-tailed) the cup that had been located behind the barrier during baiting when the removed cup was baited and empty, respectively. Focusing exclusively on the first trial of each of the conditions depicted on Table 4 revealed that subjects selected the cup that had been located behind the barrier during baiting above chance levels in all conditions, Binomial test: $p < 0.05$, 1-tailed, in all four types of trials: shown+empty: 18/23; shown+baited: 20/23; not shown+empty: 16/23; not shown+baited: 16/23.

The GEE model that included the three factors (Species, Contents shown, Contents type), their interactions and the trial number as covariate fit the likelihood of selecting the cup located behind the barrier during baiting better than a model without them, *QIC*: 1167.53 vs. *QIC*: 1192.84, N=1103, Table 5. Re-running the model after eliminating the non-significant terms improved the model's fit, *QIC*: 1162.22, N=1103, and confirmed the significant effects of Contents type, $\chi 2=19.32$, df=1, $p < 0.001$, and Contents type x Contents shown ($\chi 2=15.24$, df=1, $p < 0.001$), but not Species x Contents shown, $\chi 2= 6.88$, df=4, $p < 0.14$.

Table 5

Figure 6 presents the likelihood of subjects selecting the cup that had been located behind the barrier during baiting as a function of the Contents type and Contents shown. When the removed cup was empty, subjects were more likely to select the cup that had been behind the barrier if they had been shown the contents of the removed cup, $\chi^2 = 4.56$, df=1, $p = 0.017$, 1-tailed. In contrast, when the removed cup was baited, subjects were less likely to select the cup that had been behind the barrier if they were shown the contents of the removed cup, $\chi^2 = 18.60$, df=1, $p < 0.001$, 1-tailed.

Figure 6

Discussion

Subjects showed an overall preference for the cup that had been hidden behind the barrier when baiting took place, thus replicating the findings of Experiment 1. More importantly, apes' preference for this hidden cup decreased when subjects were shown that the removed cup was baited but it increased when they were shown that the removed cup was empty. This means that information about the contents of the cup modulated subjects' preference for the cup that had been hidden behind the barrier.

Preference modulation for the hidden cup is difficult to explain based on the 'avoid the empty cup' hypothesis because this hypothesis does not predict that the preference for the hidden cup will change as a function of the contents of the removed cup. It can only be explained if subjects see the food in the removed cup (or absent from it) as relevant information for solving this task. Similarly, the idea that subjects simply prefer the cups that were hidden behind the barrier also falls short as an explanation because it does not predict that preference will change as a function of the contents of the removed cup. This modulation makes sense only if the subjects establish a connection between the removed food item and the food item that remains. This finding is consistent with the literature on object individuation and object permanence, with subjects having expectations about where food items might be located after invisible baiting and visible displacements. Moreover, this finding reinforces the notion that expectations about the contents of the cups is a basic component of the inferences that subjects made in this task.

General discussion

Great apes faced three identical opaque cups on a platform with two having been located behind a barrier during baiting. After the experimenter revealed the identity of the empty cup that had been located behind the barrier, subjects preferentially selected the other cup that had been located behind the barrier over the cup whose contents had not been revealed either (Experiment 1). This suggest that subjects tracked the displacement of the food item and anticipated its potential locations. Even though subjects could have potentially identified the baited cup in the control condition in Experiment 1 by using (or learning to use over repeated trials) heuristics commonly invoked as alternative strategies to object knowledge (i.e., touching the cups, proximity to the barrier), they failed to do so.

In Experiment 2, the experimenter revealed the contents of one of the cups (baited in half of the trials) that had been behind the barrier during baiting but always removed it before the subject's choice. Thus, once again subjects had to choose between two cups whose contents was unknown. Again, subjects preferred the cup that had been located behind the barrier but, crucially, their choices were modulated by the observed contents of the removed cup. In particular, apes showed a stronger preference for the remaining cup that had been behind the barrier if they saw that the removed cup was empty rather than baited.

Neither the 'avoid the empty cup' hypothesis nor the use of various heuristics commonly invoked as alternatives for object knowledge in object displacement tasks can satisfactory explain the current results. First, subjects selected the baited cup out of three cups, one that they had seen to be empty and two that had not been opened (Experiment 1) or even after eliminating the empty cup (Experiment 2). According to Schmidt and Fischer (2009), this feature already represents an improvement over the original cup task. Furthermore, the current results corroborate previous studies showing that apes can infer the location of hidden food without seeing an empty cup (e.g., Call, 2006; Hill et al., 2011; Premack & Premack, 1994). Second, what they saw being removed in Experiment 2 modulated their preference for the two remaining cups, which means that the contents (or lack thereof) of the removed cup, not the sight of an empty cup, controlled apes' responses. Other heuristics or their combination also provided incomplete explanations. Proximity to the barrier during baiting is not sufficient because it does not explain modulation observed in Experiment 2. Additionally, subjects failed to use the proximity of the barrier in combination with touching (or not touching) the cups to locate the baited cup in control trials. This is not surprising because using single arbitrary cues, let alone combining them in a conditional discrimination is notoriously difficult for apes, typically requiring dozens and even hundreds of trials (Call, 2006; Hanus & Call, 2011; McGuire & Vonk, 2018).

Instead, expectations about the possible location of the food item emerged as a key component to explain subjects' choices. This suggests that great apes may choose the other cup because they expect the food to be there, which is one of the most basic forms of inference. This result is completely consistent with the existing evidence on object individuation, stage 6 object permanence and inferences using two containers and two types of food items (see Voelter & Call, 2017 for a review). The current tasks share a number of features with the original 2-cup task. All three tasks use the sight of the empty cup or the contents of the removed cup to trigger the inference. But they also differ in terms of their complexity. On the one hand, the current tasks are more complex than the original 2-cup task because they involve three cups (but see Paukner et al., 2009 for versions of the basic task with three cups) whose contents has not been revealed for two of them. On the other hand, they are simpler than the 2-cup 2-item task (Premack & Premack, 1994) because they only involve one type of food and the subject sees the contents of the eliminated cup, thus potentially reducing the representational demands. However, to what extent complexity in terms of the number of elements translates into difficulty is something that future studies will need to address. Currently, it seems safe to assume that the current tasks might fall between the original 2-cup task and the 2-cup 2-item task in terms of difficulty.

Mody and Carey (2016) proposed another explanation besides the avoiding the empty cup heuristic that does not require logical reasoning, at least not in its strongest sense. According to these authors, apes may have reasoned that the food may be located in cup A or in cup B, without necessarily connecting the two. Whereas logic requires that the two events are connected (if not in A the food *must* be in B), Mody and Carey's (2016) alternative explanation does not require this crucial connection. Mody and Carey (2016) tested 3- to 6-year-old children in a more complex variation of the cup task. They presented children with two pairs of containers, each pair behind a barrier. They showed children that they placed a toy inside one of the containers of each pair but without revealing its exact location. One can think of this version as a "double 2-cup 1-item" task. Upon removal of the barriers, children were shown the empty container in one of the pairs but not the other and they were allowed to choose one of the four containers available. Only older children managed to find the toy above chance levels, and even then, surprisingly, at not a very high level. According to Mody and Carey (2016), a crucial aspect that makes theirs a truly inferential task is understanding that the likelihood of obtaining a toy in a container is linked within but not between pairs. In other words, although initially each container within a pair has a probability of 0.50 of holding the toy, upon revealing the identity of the empty cup, the other cup necessarily increases to $P=1$, it does not remain at $p=0.50$.

Most previous studies investigating inferential / statistical reasoning in nonhuman animals had used probabilities that did not change during the course of a trial (but see Eckert et al., 2018). In fact, some evidence from two previous studies suggest that apes do conceive probabilities in a more fixed manner than humans (Haun et al., 2011; Hanus & Call, 2014). In these studies, apes chose from two sets of cups whose numbers and the quantity of food hidden varied over trials. For instance, Hanus and Call (2014) presented subjects with a choice between a set with two cups holding 1 food item (1 cup baited, 1 cup empty) and another set of six cups holding 1 piece of food (1 cup baited, 5 cup empty). Subjects' choices were consistent with Weber's law, which means that the probability of selecting the most favourable set varied depending on the difference between the probabilities for each set. Interestingly, in some trials one of the sets only contained one cup, which means that the food was located there with certainty. Apes, however, did not take this into account, and instead continued to apply Weber's law. In other words, a trial contrasting 2 vs. 6 cups was equivalent to one with 1 vs. 3 cups, which is consistent with the ratio, but not certainty. Leahy and Carey (2020) used this to suggest a special status for human reasoning about probabilities, one that considers certainty and where probabilities are adjusted depending on what is empty.

Pepperberg et al. (2019) tested an African grey parrot (Griffin) using the 4-cup method designed by Mody and Carey (2016). They found that although Griffin initially failed the task twice (two separate attempts involving multiple trials), he eventually passed it, selecting the cup next to the empty one on 94% of the trials (Exp. 2). The authors attributed his initial failures to a bias caused by external factors to the task (preference for a particular color and/or his health status at the time of the test). However, it is conceivable that Griffin may have benefited from his prior experience with the task, and perhaps had learned a heuristic to solve that task which did not require inference. The authors tested the possibility that Griffin had simply learned to select the cup located next to the cup that was shown to be empty. Their results did not support the use of this heuristic and they concluded that Griffin had indeed used inferential reasoning to solve the task, although they conceded that it was unclear whether he did so by entertaining notions of possibility or certainty.

More recently, Ferrigno et al. (2021) tested nine olive baboons in the four-cup task except that instead of revealing the identity of one of the cups, they allowed the baboons to make two choices. The first choice served to reveal an empty or a baited cup in one of the two sets, and the second choice informed researchers about whether baboons switched sets depending on what their first search had uncovered. The authors tested nine baboons but only four passed two prerequisite tests: the basic 2-cup 1-item task and an updating working memory task. During the test, three of the four baboons upon finding an empty cup preferentially selected the other cup in the same set as opposed to one of the other cups in the alternative set. Moreover, they were more likely to point before the experimenter offered them a second choice (so-called pre-pointing behavior) when they uncovered the empty rather the baited cup in their first choice (72% empty vs. 9% baited). The authors interpreted this behavior as a confidence indicator for finding the baited cup. This type of response is reminiscent of the increase in choices toward the cup that had been behind the barrier during baiting after apes in the current study saw that the removed cup was empty.

Ferrigno et al.'s (2021) findings are intriguing but should be interpreted with caution for two reasons. First, when the baboons found the baited cup in their first search (thus depleting the food in that set), they did not preferentially select one of the cups in the other set, but instead they chose randomly, selecting the empty cup in that same set in 33% of the trials. Second, subjects received a substantial number of trials (about 240) in each of the two pre-tests and the test, and their analyses revealed that subjects improved their performance over time, thus raising the possibility that baboons had learned how to respond during the test. Although the authors addressed this issue analytically, e.g., the learning effect was not detected in trials in which subjects' first choice uncovered the empty cup (which as the authors pointed out are the trials most comparable to Mody & Carey's (2016) original design), Ferrigno et al. (2021) did not report whether the baboons were above chance in the first test session (or the first 24 trials in which subjects selected the empty cup). They did include an analysis assessing first trial performance, but with just three subjects it is unclear how one can determine that baboons performed above chance in the first trial.

To the best of my knowledge, the four-cup task has not been tested with apes yet. But the results of Hanus and Call (2014) seem to indicate that chimpanzees may not be able to solve it because chimpanzees did not distinguish between one option with P=0.50 and another with P=1. The results of Experiment 2, however, suggest that apes might not be so rigid in the way they conceive probabilities as the previous studies seem to suggest. Recall that subjects changed their preference for the hidden cup depending on what they saw removed from the platform. If they saw that the removed cup was baited (recall that the removed cup had always been hidden behind the barrier during baiting), they decreased their preference for the hidden cup, but if it was empty, they increased it, albeit much less so than in the other case. This suggests that apes might have linked the probability between the two cups and revised them when confronted with new evidence. Watson et al. (2001) reported that children who had witnessed the invisible displacement of the target under multiple cups engaged in a sequential search. Crucially, their search speed increased with each cup that they found empty. The authors suggested that children did so because their certainty about the baited location increased after every choice that returned an empty container. In contrast, dogs displayed no such acceleration upon encountering empty containers, in fact they showed a tendency to decrease their search speed, consistent with an extinction strategy. As far as I know, this study has not been done with apes/primates, but the modulation observed in Exp. 2 suggests that they may be more similar to children than dogs.

Although the results of Exp. 2 are suggestive of a link between the likelihood of obtaining the food under each of the cups, there are several reasons to be cautious. First, Mody and Carey's (2016) task and the current task are different, and therefore their results cannot be directly compared. Second, the magnitude of the change in preference compared to the control condition depended on whether they saw the food being removed or not. More specifically, the decrease in preference after witnessing the food's removal was more substantial in absolute terms than the increase in preference after seeing that no food had been removed. One possible explanation for this asymmetry is that apes might be more sensitive to losses than to gains. Another possibility, not mutually exclusive with a loss aversion, is motivational in nature. Once the food was gone apes lost interest and chose randomly between the two cups. Note, however, that I did not observe an increase in trials without response as a function of condition. But even if this were the case, it would still mean that subjects understood that the food that was just removed was the food that went behind the screen during the initial baiting. This would be entirely consistent not only with the evidence on object permanence and inferential reasoning in the literature but also with the data on object individuation, which demonstrates that apes and macaques track not only the location but also the number of items that are hidden (Mendes et al., 2008, 2011; Santos et al., 2002; Phillips & Santos, 2007; Tinklepaugh, 1928, 1932). Third, the asymmetry could have been caused by apes' high preference (80%) for the hidden cup, a fact that was apparent in both experiments. In other words, whereas they could only increase in preference by 20 points when the food was not removed, they could decrease 80 points (or just 30 if one considers chance responding) after they saw the food being removed. One way to correct for this inherent asymmetry in the design is to find a task with a baseline closer to 50%, something that could be achieved by varying the quality and the quantity of items under the cups.

Much progress has been made in the last decade towards mapping out the distribution of inferential abilities across taxa (see Voelter & Call, 2017). However, without the proper controls, it is impossible to conclude that inference is at work. Therefore, much of the work has been devoted to distinguish inferential from non-inferential processes – an analytic approach that is unsurprising because the same strategy has been followed in other areas such as object permanence. It is now well-established that proper control conditions (aimed at ruling out a variety of heuristics) are needed to conclude that subjects display stage 6 object permanence. It is difficult to prescribe which specific controls are the most suitable for inferential tasks because controls should be tailored to 1) the particular features of the inferential task being used and 2) the non-inferential strategies being tested. In Exp. 1, I used the control condition to test the possibility that subjects may have used a combination of touching the cups and the location of the cups behind the barrier to solve the task. This control condition also assessed whether subjects used experimenter-given cues to solve the task. In contrast, the control conditions in Exp. 2 focused on different aspects. The reveal baited condition acted as a control condition for the reveal empty condition (which implemented the original idea of the 2-cup 1 item task). Additionally, the pair of non-revealed conditions provided a preference baseline for the cup that was located behind the barrier during baiting.

Equally important to ruling out non-inferential strategies, but far less studied, is the type of inference that individuals use to solve the 2-cup 1-item task, or any other task for that matter. Based on the degree of certainty about the food's location, one can distinguish at least three basic levels of inference of increasing strength (Call, in press; see also Pepperberg et al., 2019). Note that the labels that I used to distinguish the three levels of inference (abduction, induction and deduction) originate in the philosophical literature but other authors use them with different meaning in the comparative literature. I consider inference by abduction (A empty, perhaps B) the weakest form of inference, based on simply forming an expectation about the food's location – heuristics do not even require forming an expectation. Finding that cup A is empty, individuals expect to find the food in the other cup. However, finding cup A empty does not alter the strength of the expectation of finding the food under cup B, which is precisely the key feature of the next level, inference by induction (A empty, B more likely). In this case, upon finding that cup A is empty, the probability that food is located under cup B increases. This means that the probabilities of finding food under A or B are linked. Finally, inference by deduction is the strongest form of inference (A empty, B certain) whereby the likelihood of finding food under cup B upon seeing that cup A is empty is replaced with the certainty of finding the food under cup B. There is plenty of evidence for abductive inference (most studies in Voelter & Call, 2017), very few studies testing inductive inference (Ferrigno et al., 2021; Pepperberg et al., 2019, the current study) and none demonstrating deductive inference. Future studies should continue to test species to establish whether they use inference to solve the original 2-cup 1-tem task and allied tasks, and if they do, which type of inference is implicated in each case.

The results of the current study do not prove that subjects who passed the original 2-cup version in previous studies did so by using inference. Moreover, seeing an empty cup may have contributed to the responses in the original 2-cup, and even the 3-cup task in Experiment 1. However, the current results also show that merely avoiding the cup that they saw to be empty without forming expectations about the food's location does not explain the results of the two 3-cup tasks presented here, particularly those in Experiment 2. It is conceivable that subjects may have used a substantially different form of the 'avoiding the empty cup' hypothesis distinct from the original perceptually-based explanation (Paukner et al., 2006). In particular, subjects may have avoided the empty cup because they *inferred* rather than they *saw* that it was empty, but this kind of explanation would invoke an even perhaps more sophisticated form of expectation (about the absence of something) than choosing the baited cup because subjects inferred that it contained the food.

In conclusion, the 'avoid the empty cup' hypothesis whereby subjects succeed by avoiding the cup that they *have seen* to be empty cannot satisfactorily explain the results of two experiments on inferential reasoning in the great apes. Similarly, other heuristics like choosing the cups in proximity to (or behind) the barrier during baiting, or the cup that was in proximity to the barrier and touched by the experimenter before the subjects' choice cannot explain the current results either. Instead, subjects located the correct cup based on tracking its displacement behind a barrier and the sight of the empty cup (Exp. 1) or the contents of the cup that was removed (Exp. 2) before the subjects' choice. Thus, forming expectations about the location of food based on indirect evidence emerged as the best explanation for the current results, and it is likely to constitute the basis for more complex forms of inference in the spatio-temporal dimension. Moreover, modulation of preference depending on the contents of the removed cup suggests that they did not see the two cups as completely independent (it can be in A or it can be in B) but that they connected the two - food in one meant a lower likelihood of finding food in the other and vice versa. Future studies are needed to consolidate these results. Besides providing a direct test of the 'avoid the empty cup' hypothesis as the sole explanation for success in object search inferential tasks, this study aimed at providing a test that could distinguish between the various processes leading to the selection of the alternative cup with the idea of establishing solid broad taxonomic comparisons. Adding these tests to the suite of available tests of inference will allow researchers to obtain a more precise understanding of the distribution of inferential abilities in the animal kingdom. However, future studies that use these same tasks, especially when validating them for the first time with a new species, should also include the necessary controls to rule out the possibility that subjects' responses are entirely based on non-inferential processes. Mapping the distribution of inferential abilities across species requires not only distinguishing inference from non-inferential strategies, but requires a more fine-grained analysis pinpointing the type of inference that may underlie subjects' successful performance.

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Table 1

Demographic information about the subjects included in Experiment 1 and number of correct choices as a function of Condition (out of 12 possible). Bold lettering for the combined touch / no touch scores (per condition) denotes P<0.025, 1-tailed, Binomial test, P_e=0.33.

					Condition			
					experimental		control	
Name	Species	Sex	Age	Rearing	touched	not touched	touched	not touched
Joey	Bonobo	male	27	nursery	1	1	4	3
Kuno	Bonobo	male	13	nursery	**3**	**5**	2	3
Limbuko	Bonobo	male	14	nursery	**5**	**5**	3	3
Luiza	Bonobo	female	5	mother	**6**	**5**	3	4
Ulindi	Bonobo	female	16	mother	3	0	2	4
Yasa	Bonobo	female	12	mother	**5**	**6**	**4**	**4**
Alex	Chimpanzee	male	9	nursery	**5**	**6**	4	3
Alexandra	Chimpanzee	female	10	nursery	2	5	**3**	**5**
Annett	Chimpanzee	female	10	nursery	**5**	**6**	3	0
Fifi	Chimpanzee	female	16	mother	**6**	**6**	4	3
Gertruida	Chimpanzee	female	16	mother	**6**	**6**	**4**	**4**
Jahaga	Chimpanzee	female	17	mother	**6**	**4**	3	4
Bebe	Gorilla	female	30	unknown	**2**	**6**	1	3
Gorgo	Gorilla	male	28	nursery	**4**	**5**	2	3
Kibara	Gorilla	female	5	mother	**6**	**6**	2	4

Viringika	Gorilla	female	14	mother	**6**	**6**	2	4
Bimbo	Orangutan	male	28	mother	**5**	**5**	4	3
Dokana	Orangutan	female	20	mother	**3**	**6**	4	2
Dunja	Orangutan	female	36	unknown	**3**	**5**	4	2
Kila	Orangutan	female	9	mother	**5**	**5**	**3**	**5**
Padana	Orangutan	female	11	mother	**6**	**5**	2	4
Pini	Orangutan	female	21	mother	**4**	**6**	2	1
Rajah	Orangutan	female	6	mother	3	2	2	2

Table 2

Factors included in the GEE model with the likelihood of selecting the baited cup as the dependent variable (*QIC*: 689.40, N=552).

Factor	Chi-square	df	P-value
(Intercept)	3.552	1	0.059
Condition	26.666	1	0.000
Species	5.153	3	0.161
Touched cups	13.966	1	0.000
Baited location	1.685	1	0.194
Condition * Species	7.989	3	0.046
Condition * Touched cups	0.85	1	0.357
Condition * Baited location	3.036	1	0.081
Species * Touched cups	21.846	3	0.000
Species * Baited location	4.99	3	0.173
Touched cups * Baited location	0.145	1	0.704
Trial number	2.711	1	0.10

Table 3

Factors included in the GEE model with likelihood of making an error by choosing the cup that remained outside the barrier during baiting as the dependent variable, *QIC*: 233.13, N=552.

Factor	Chi-square	df	P-value
(Intercept)	0.615	1	0.433
Condition	39.910	1	0.000
Species	0.547	3	0.908
Touched cups	0.363	1	0.547
Baited location	4.542	1	0.033
Condition * Species	7.512	3	0.057
Condition * Touched cups	0.062	1	0.804
Condition * Baited location	5.683	1	0.017
Species * Touched cups	0.837	3	0.841
Species * Baited location	3.239	3	0.356
Touch * Baited location	0.662	1	0.416
Trial number	0.765	1	0.382

Table 4

Demographic information about the subjects included in Experiment 2 and number of choices directed at the remaining cup that had been located behind the barrier during baiting as a function of the contents of the removed cup and whether it was shown to the subjects (out of 12 possible). Bold lettering denotes $P<0.02$, 1-tailed, Binomial test, $P_e=0.5$.

					Content type x Content shown			
Name	Species	Sex	Age	Rearing	baited shown	baited not shown	empty shown	empty not shown
Fimi	Bonobo	female	6	mother	7	7	**10**	8
Kuno	Bonobo	male	18	nursery	5	**10**	**11**	9
Lexi	Bonobo	female	15	mother	**10**	**10**	**12**	**11**
Yasa	Bonobo	female	17	mother	**10**	**10**	**11**	9
Alex	Chimpanzee	male	13	nursery	8	**12**	**11**	**11**
Alexandra	Chimpanzee	female	15	nursery	8	9	**12**	**11**
Daza	Chimpanzee	female	29	nursery	6	7	6	7
Fraukje	Chimpanzee	female	39	nursery	7	**11**	**11**	**12**
Frederike	Chimpanzee	female	41	mother	8	9	9	9
Jahaga	Chimpanzee	female	22	mother	9	**12**	**12**	**12**
Jeudi	Chimpanzee	female	49	unknown	5[1]	**11**	**10**	8
Kara	Chimpanzee	female	10	mother	8	9	**11**	8

Kofi	Chimpanzee	male	9	mother	**10**	**12**	**12**	**11**
Lobo	Chimpanzee	male	11	mother	9	**10**	**10**	**10**
Lome	Chimpanzee	male	14	mother	8	**11**	**11**	**12**
Sandra	Chimpanzee	female	21	mother	**11**	**11**	**10**	**10**
Bimbo	Orangutan	male	34	mother	6	**11**	**12**	9
Dokana	Orangutan	female	26	mother	6	8	**10**	9
Padana	Orangutan	female	17	mother	**12**	9	8	**10**
Pini	Orangutan	female	26	mother	8	**12**	**12**	**12**
Rajah	Orangutan	female	11	mother	7	**11**	9	**11**
Suaq	Orangutan	male	5	mother	5	7	7	6
Tanah	Orangutan	female	5	mother	5	7	7	6

[1] based on 11 trials

Table 5

Factors included in the GEE model for the likelihood of selecting the cup that that was located behind the barrier during baiting as the dependent variable (QIC: 1167.53, N=1103).

Factor	Chi-square	df	P-value
(Intercept)	38.553	1	0.000
Contents shown	2.004	1	0.157
Contents type	23.713	1	0.000
Species	3.158	2	0.206
Contents shown * Contents type	16.536	1	0.000
Contents shown * Species	6.022	2	0.049
Contents type * Species	1.799	2	0.407
Contents shown * Contents type * Species	1.505	2	0.471
Trial number	0.001	1	0.976

Figure 1

Steps followed in the experimental condition of Experiment 1. Not depicted is the touch/no-touch manipulation before the subject chose. The control condition is identical to the experimental condition except that the experimenter did not lift the cup in step 5.

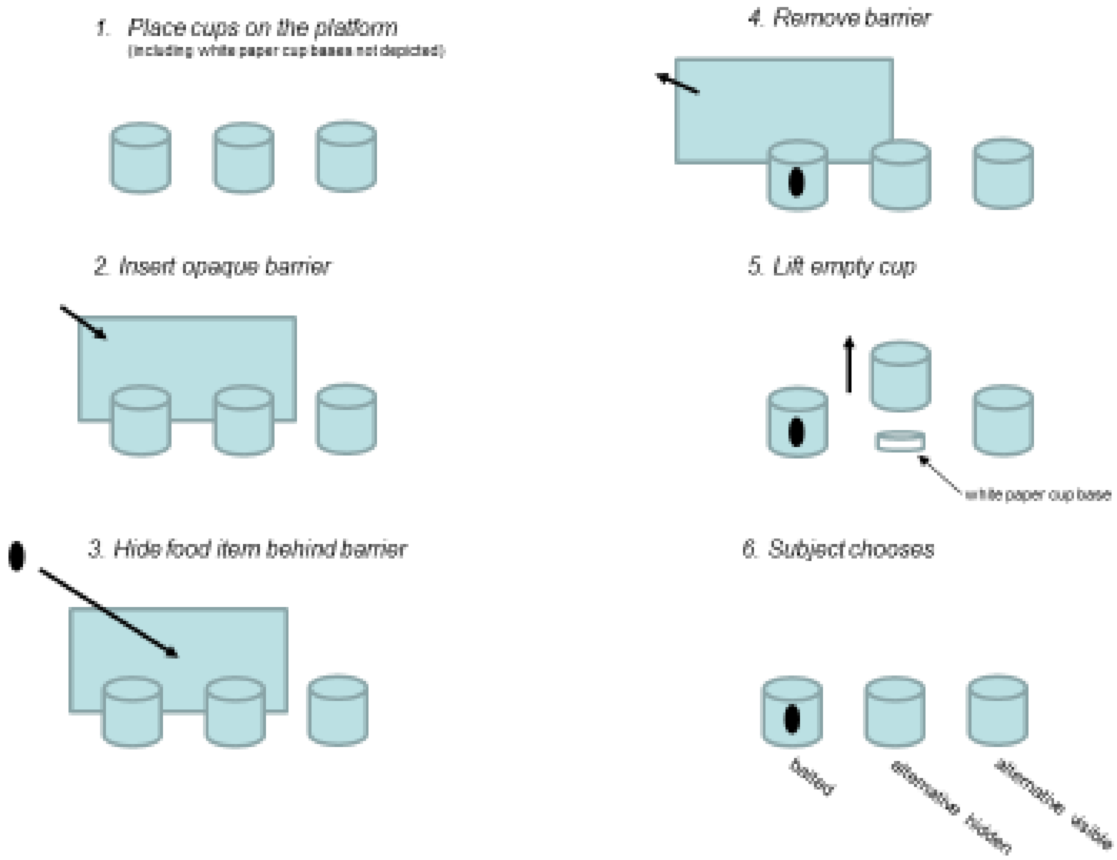


Figure 2

Proportion (±95% CI) of choices aimed at the baited cup as a function of Species and Condition. ** P<0.01, *** P<0.001.

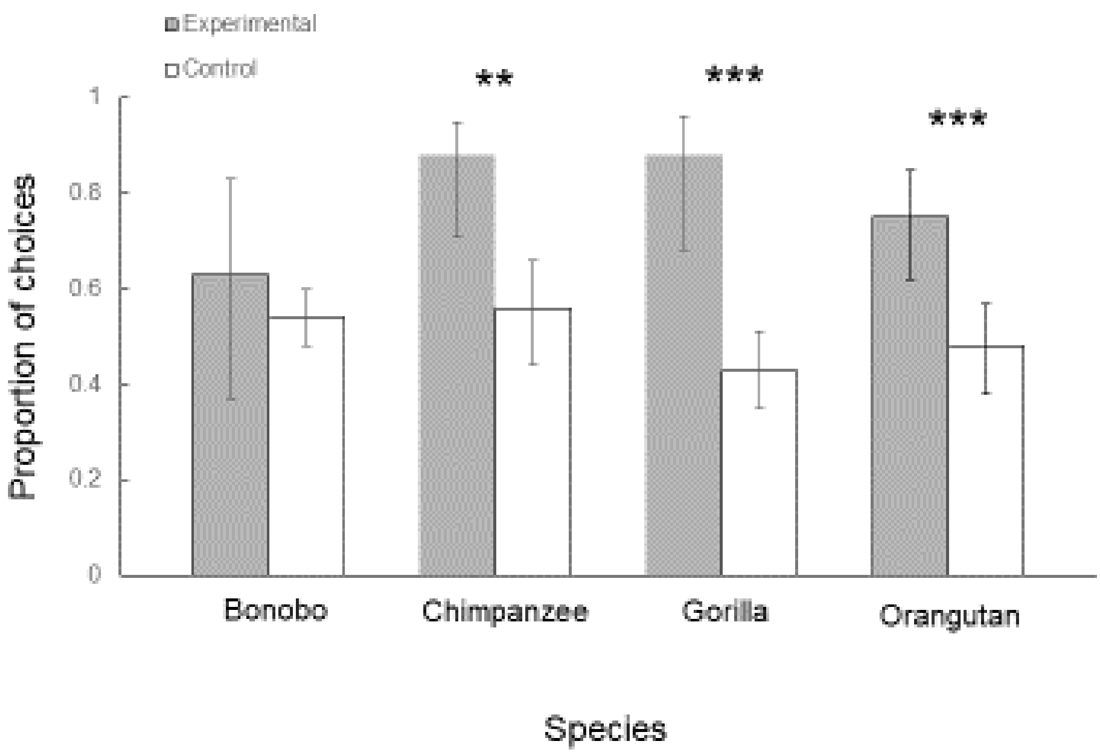


Figure 3

Proportion (±95% CI) of choices aimed at the baited cup as a function of Species and Touch. *** P<0.001.

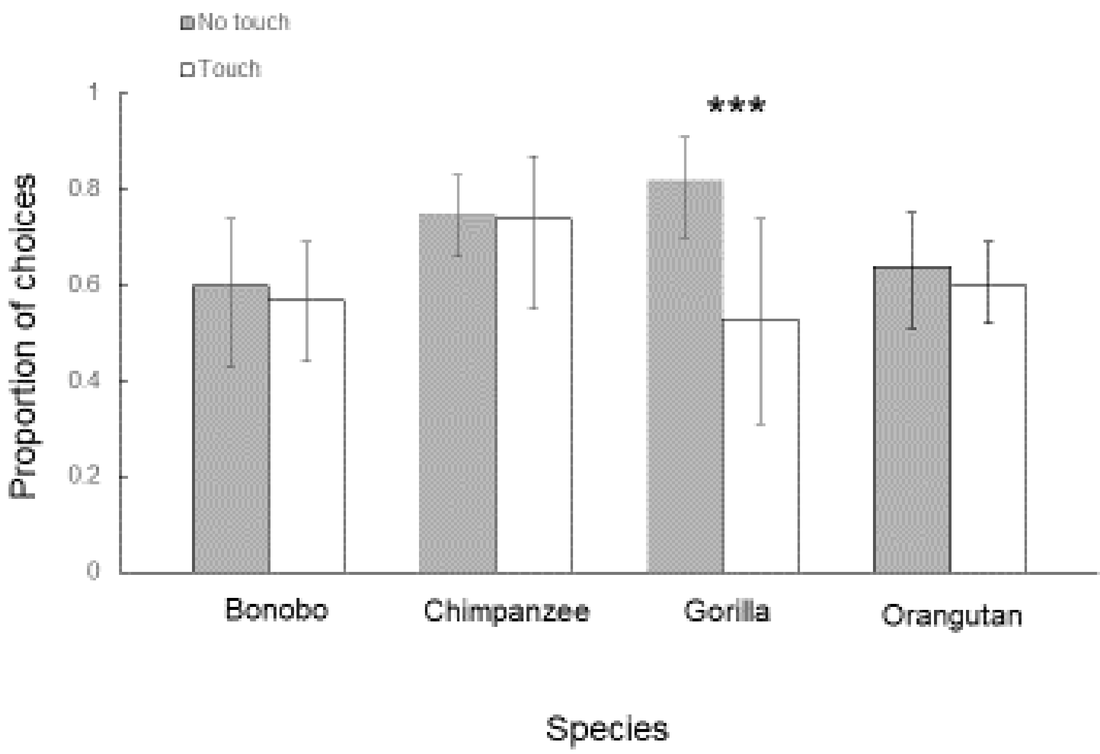
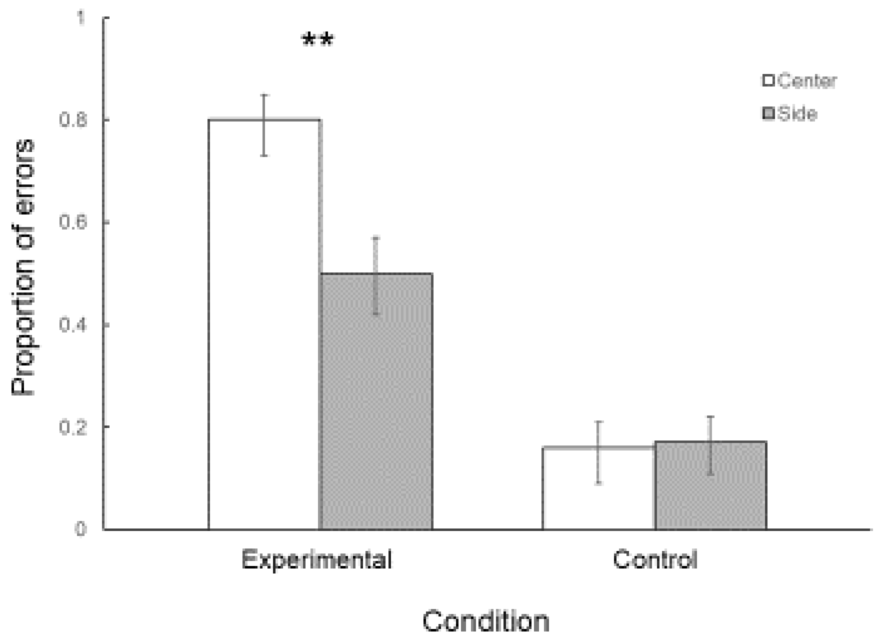


Figure 4

Proportion (±95% CI) of errors caused by choosing the cup that had been outside the barrier during baiting as a function of Condition and Baited location, ** P<0.01. Total number of errors: experimental condition=64, control condition=136.



Note. When the baited cup was in the center of the platform the two empty cups were non-adjacent to each other whereas when the baited cup was in one of the sides, the two empty cups were adjacent to each other.

Figure 5

Procedural steps and resulting conditions in Experiment 2.

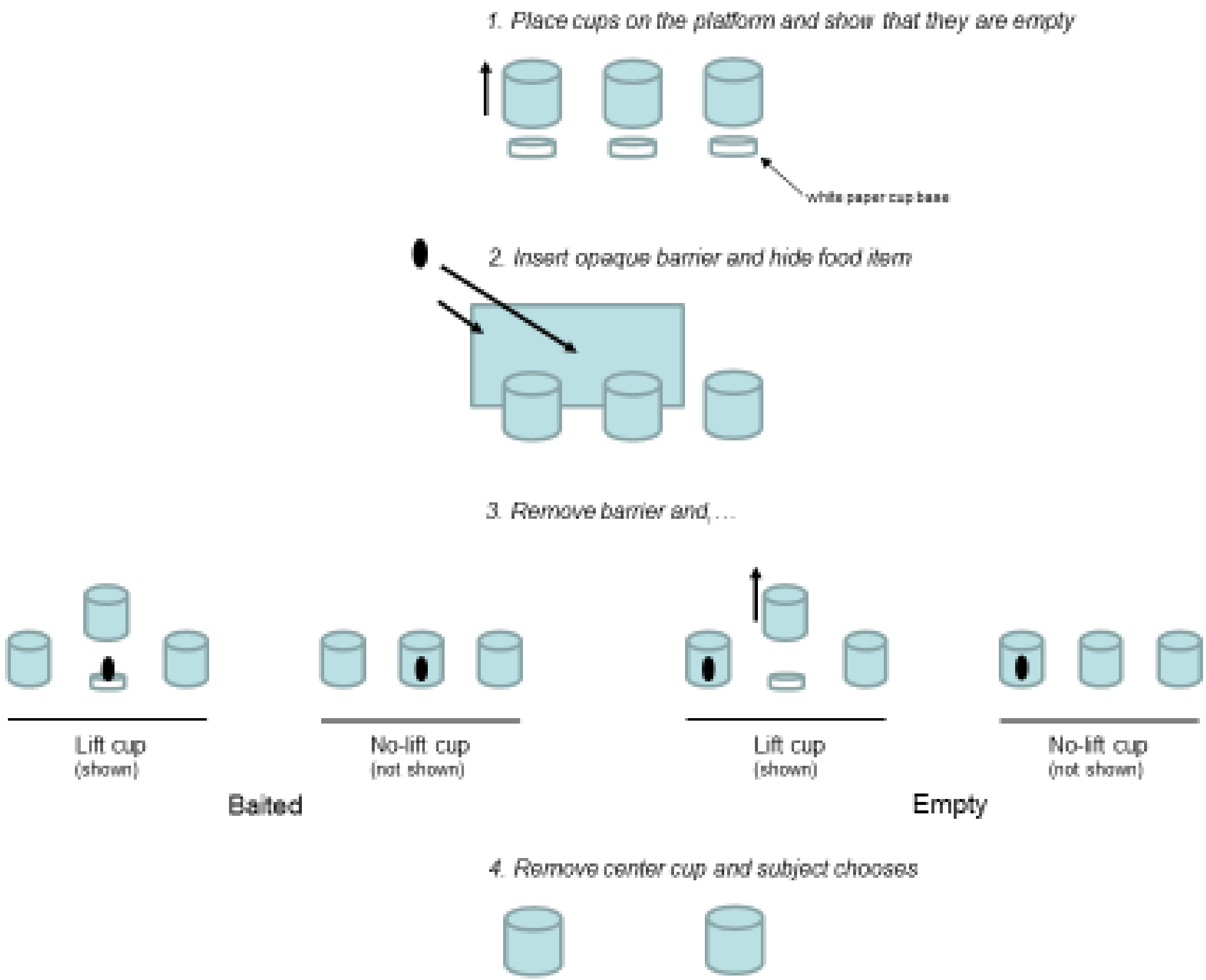


Figure 6

Proportion (±95% CI) of choices aimed at the remaining cup that was located behind the barrier during baiting as a function of the removed cup's Contents type and whether it was shown to the subject. * P<0.05, *** P<0.01, 1-tailed.