

# Chimpanzee problem-solving: contrasting the use of causal and arbitrary cues

Daniel Hanus · Josep Call

Received: 6 December 2010 / Revised: 11 May 2011 / Accepted: 19 May 2011 / Published online: 7 June 2011  
© Springer-Verlag 2011

**Abstract** Humans are able to benefit from a causally structured problem-solving context rather than arbitrarily structured situations. In order to better understand nonhuman causal cognition, it is therefore important to isolate crucial factors that might differentiate between events that follow a purely spatial and temporal contingency and those that hold a “true” causal relationship. In the first of two experiments, chimpanzee subjects were required to detect a bottle containing juice from five opaque bottles of equal shape and size. In the *causal condition*, the juice bottle looked identical to the other four bottles, only it was much heavier than the others. In the *arbitrary condition*, the weight of all five bottles was identical, but the juice bottle was color-marked differently. Since bottle opening was made difficult (and therefore costly), the question was whether subject’s manipulative behavior would be random or somehow influenced by the nature of the provided information. Our results show that subjects detected and opened the juice bottle significantly faster when weight was the discriminating feature (*causal condition*) compared to situations in which the discrimination was necessarily based on a color-cue (*arbitrary condition*). Experiment 2 ruled out the possibility of a general learning bias toward tactile rather than visual information in chimpanzees. When tested in a simple exchange paradigm that prevented any use of causal information, no predominance of a tactile cue (weight) over a visual cue (color) could be found. Furthermore—and in contrast to the *causal condition* in Experiment 1—no learning occurred during the course of Experiment 2, neither in the weight nor in the color condi-

tion. We therefore conclude that chimpanzees can more easily determine the content of an object based on its causal properties compared to situations in which the only available information is a pure arbitrary regularity. This supports the view that chimpanzees’ causal cognition does not rely on mere perceptual information but also on structural abstraction about their physical environment.

**Keywords** Problem-solving · Causal cognition · Chimpanzees · Arbitrary cues · Causal cues

## Introduction

Animals can exploit a variety of visual, tactile, auditory, or olfactory cues to detect the presence of food (e.g., Krebs et al. 1993; McFarland 1993). However, cues vary according to the nature of the relation between their presence and the presence of food (Call 2006a). Whereas some are arbitrary relations by virtue of the cues’ covariation with the presence of food (e.g., a light indicates the presence of food), others are causal in the sense that the cues are directly caused by the presence of the food. Typically, these causal relations are grounded on physical laws that govern how objects interact with each other. For instance, an object placed off-center underneath a tray invariably causes the tray to acquire a certain slope, or a solid object shaken inside a cup causes a rattling noise. Both the slope of the tray and the rattling noise constitute causal cues. Note that under normal circumstances and without deceptive manipulations such causal cue–outcome relations are compulsory, given that it is physically impossible for the inclined tray to have nothing underneath it (and for the flat tray to cover the food item), or for the noisy container to be empty (and for the noiseless one to contain solid food items).

D. Hanus (✉) · J. Call  
Max Planck Institute for Evolutionary Anthropology,  
Deutscher Platz 6, 04103 Leipzig, Germany  
e-mail: hanus@eva.mpg.de

Recent studies have shown that great apes can use causal cues such as the inclination of a board, the presence of a hole through which the food might fall, the noise made by a reward inside a shaken cup, or the displacement of a balance beam to infer the presence of food (Call 2004, 2006b; Hanus and Call 2008; Martin–Ordas and Call 2009).

At the same time, apes were unable to use cues that bore an arbitrary relation to the reward, despite repeated opportunities to use them and despite the close perceptual similarity between causal and arbitrary cues. For instance, subjects showed no more preference for a wedge (displaying the same slope as the inclined board) that covered a hole containing a reward than for a flat board that covered an empty hole, even after repeated trials. Thus, although causal and arbitrary cues may provide identical perceptual information, they differ crucially in their predictive power and the inferences they allow—which is reflected in the different performances these cues evoke.

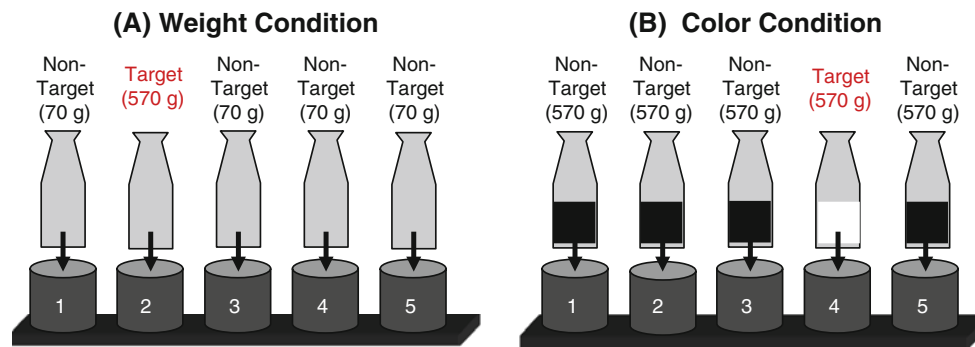
Exploiting the greater predictive power of causal cues can be particularly advantageous when edible parts of an object are not directly visible and hard to process, for example in heavily defended or encased foods (e.g., nuts). For instance, both color and weight are two possible indicators of the presence of an edible kernel inside a nut. However, whereas weight has a causal relation to the presence of a kernel—a light nut cannot contain an intact kernel—the right color and the presence of a kernel are not causally related in this case, because the nut might have been emptied by some insect. Hanus and Call (2008) focused precisely on the causal–arbitrary distinction instantiated by the effect that the presence of food may have on the weight of an object. Chimpanzees had to infer the location of food based on the slope of a beam (initially at equilibrium) after food had been placed in one of two cups balanced on each of its ends. From the first trial onwards, subjects preferentially chose the cup on the lower side of the balance. Crucially, they did not show this preference in two control tests in which the cups were either mounted on a fixed inclined ramp mirroring the position of the cups at the end of the experimental trial or in which the experimenter (not the reward) caused the balance to tilt in one direction.

Subjects in all of these studies had a relatively passive role, restricted to witnessing an event and making a choice between two containers. Another important aspect to address is how subjects actively deploy their knowledge about weight in more manipulative tasks, as would appear under natural conditions, where primates are not just passive observers. Visalberghi and Néel (2003) demonstrated that two captive capuchin monkeys could learn to use the sound and/or weight of a nut to infer its content (full or empty). The authors concluded that the monkeys successfully adapted their perception and modified their behavior in order to discriminate full from empty nuts before investing

in a costly opening process. However, it is unclear whether subjects made causal inferences or rather learned to select nuts of a certain weight, with weight simply being a discriminative arbitrary stimulus. What is needed is an assessment (and a comparison) of how quickly subjects would solve a comparable problem solely grounded on arbitrary relations.

The goal of the current study was to investigate whether chimpanzees were able to take advantage of a causally structured problem compared to an arbitrary one in a task designed to emulate an active foraging situation similar to that used by Visalberghi and Néel (2003). Unlike that study, however, the current study explicitly included two types of cues that varied in their relation to the reward (causal vs. arbitrary). In the first of the two experiments, chimpanzees were required to find a bottle containing fruit juice (target bottle) from five opaque bottles of equal shape and size. In the *causal condition*, all five bottles looked identical, but the juice bottle was much heavier than the other four empty bottles (target bottle = 570 g, nontarget bottles = 70 g). In the *arbitrary condition*, the weight of all five bottles was the same (570 g), since the four nontarget bottles were filled with the same amount of water; the juice bottle, however, was marked differently (target bottle = white, nontarget bottles = black). In other words, both conditions provided completely reliable cues for finding the desired juice bottle, with the crucial difference that the indication was either of a causal (weight) or arbitrary nature (color). We selected weight and color as cues because Schrauf and Call (2009) showed that bonobos, gorillas, and orangutans were not more likely to learn one better than the other when both held an arbitrary (but 100% predictive) relation to the reward. Experiment 2 was explicitly designed to control for a general tendency in chimpanzees to learn tactile cue–outcome associations (weight  $\Rightarrow$  food) better/faster than visual cue–outcome associations (color  $\Rightarrow$  food), given that no causal inference could be made in both cases. We used the same stimuli (bottles) as in Experiment 1 with the crucial difference that the specific weight was not caused by the presence of food (juice or water) but by inaccessible, uneatable material inside the bottles (gypsum). Instead of opening the correct bottle, subjects had to exchange the target object with a human experimenter in order to receive a food reward (juice).

Our main hypothesis for Experiment 1 was that if subjects treated causal information preferentially, they would perform better in the *causal condition* (weight) than in the *arbitrary condition* (color). In particular, we would expect that after manipulating the bottles, they would open the correct one first (or earlier) in the weight condition compared to the color condition. If however subjects only formed associative connections between certain features



**Fig. 1** Plastic repository in which the five bottles were placed during Experiment 1 (opening paradigm) and Experiment 2 (exchange paradigm). While resting in the repository only the *top half* of each bottle was visible. **a** Weight condition: position of the target bottle (*heavy*)

and the four nontarget bottles (*light*) was randomized and counterbalanced across sessions. **b** Color condition: position of the target bottle (*white*) and the four nontarget bottles (*black*) was randomized and counterbalanced across sessions

and outcomes during the course of the experiment, neither condition should differ with regards to the subjects' order for opening the bottles. Furthermore, if tactile information (i.e., weight) is per se more salient (thus fostering faster learning) than visual information regardless of its causal structure Experiment 2 should detect such a learning bias.

### Experiment 1: opening paradigm

#### Materials and methods

#### Subjects

We tested eight chimpanzees (four males, four females) with ages estimated between 6 and 10 years (mean = 8.25, SD = 1.09). All chimpanzees were wild-born, orphaned at a young age, and rescued and sent to the Ngamba Island Sanctuary, Uganda, where they lived in a social group at the time of testing. Although subjects had participated in other cognitive tasks prior to the current study, none of these tasks involved color or weight discrimination. All subjects were tested individually and were never deprived of food or water.

#### Materials

Five identical 500-ml plastic Coca-Cola bottles with their corresponding lids served as stimuli. They were rendered opaque by being wrapped with gray duct tape. Bottles were filled with either strawberry juice (target), water (nontarget), or left empty (nontarget), depending on the experimental condition. Juice and water filled bottles weighted 570 g whereas empty bottles weighted 70 g. During the preparation phase of the test, we presented the bottles on a wooden platform (100 cm × 40 cm) in front of the subject. During the manipulation phase, the bottles were placed in

an opaque plastic repository that covered the bottom part of each bottle (see Fig. 1). This made the salience of the cues in the two test conditions (weight and color; see below) more comparable because subjects could not see or feel any difference between the five bottles until they had lifted them.

#### Procedure

**Pretest** Prior to the test, we assessed whether chimpanzees preferred juice when given the choice between (a) the same amount of juice and water or (b) juice and nothing/air. We presented subjects with two transparent bottles, one filled with juice and the other one either empty (four trials), or filled with water (four trials). Subjects immediately received the content of the bottle they indicated. We administered trials of both conditions in an alternating fashion (e.g., juice vs. empty ⇒ juice vs. water ⇒ juice vs. empty ⇒ and so forth). Only those subjects who chose the juice over the water or the empty bottle in the last two trials advanced to the test.<sup>1</sup>

**Test** Each test trial consisted of a preparation phase and a subsequent manipulation phase.

During the preparation phase, the experimenter (E) sat facing the subject, separated by mesh, with five opaque bottles resting on a platform between them. All bottles were initially open, and E turned them upside-down so that the subjects could see that they were empty. There were two conditions: weight and color. In the preparation phase of the weight condition, E filled one of the bottles with juice (target), leaving the four remaining ones empty (nontargets). In the preparation phase of the color condition, E filled one bottle with juice (target) and the four remaining

<sup>1</sup> Only one subject from the original test population had to be excluded because she did not fulfill the pretest criteria.

ones with water (nontargets). Bottles were filled up to the top in order to avoid auditory cues when shaken. The initial placement of the five empty bottles was randomized and the juice was always poured into the first bottle on the left. After filling the bottles, E screwed on their lids and sealed them with adhesive tape to make them harder (and hence more costly) to open. Then, E placed all bottles in a bucket and took them to a neighboring room out of the subject's view. Up until this moment, subjects had witnessed the entire preparation procedure.

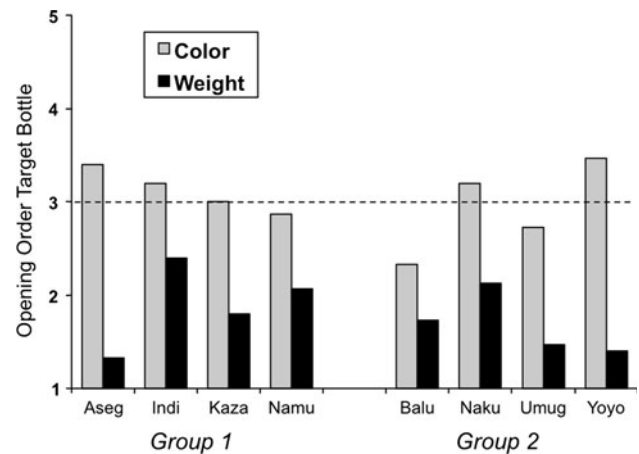
Then, the manipulation phase began. In the weight condition, E lined up all five bottles in a repository (see Fig. 1) inside an empty testing room, with the position of the target bottle randomized and counterbalanced across trials. In the color condition, E labeled the lower part<sup>2</sup> of the bottles with different colors before placing them in the repository. The juice bottle was labeled with a white mark and the four water bottles with a black mark. In both conditions, all bottles were doused with some juice in order to preclude any gustatory or smell cue.

At that point, the subject was allowed to enter the testing room. We coded the order in which the subject opened or tried to open the bottles to gain access to their contents. Thus, our dependent measure was the order in which the bottles were opened, not the order in which the bottles were touched or lifted. Both actually opening the bottles (i.e., successfully removing the lids) and attempting to destroy the bottles' opaque coating in order to visually verify the contents were coded as "opened".

Subjects received both conditions successively (15 trials per condition) with the order of presentation counterbalanced across subjects. Group 1 (four subjects) started with 15 trials of the weight condition followed by 15 trials of the color condition, whereas group 2 (four subjects) received them in the opposite order. All subjects received only two trials per day, resulting in 8 testing days per condition and 16 testing days in total. There was at least a 1-day break before conditions were swapped. All data were collected between November and December 2007.

## Results

If subjects treated the bottles randomly, the target bottle should be opened third on average. Within the first testing block (Trial 1–15), subjects in the weight condition (Group 1) opened the target bottle significantly earlier than would be expected by chance (Mann–Whitney exact test:  $U = 0$ ,  $n_{\text{weight}} = 4$ ,  $n_{\text{chance}} = 4$ ,  $P = 0.029$ , two-tailed). In contrast, the subjects in the color condition (Group 2) opened the bottles in an order that did not differ from chance



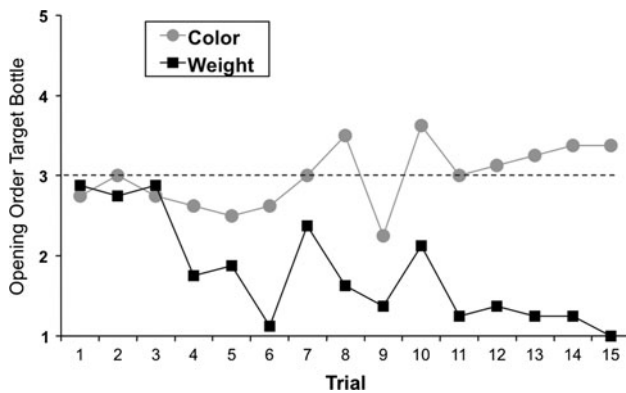
**Fig. 2** Average opening order of the target bottle for each individual across all 15 trials of Experiment 1. *Gray bars* represent subject's performance in the color condition (arbitrary cue); *black bars* represent the performance in the weight condition (causal cue). The *dashed line* indicates a random opening order

expectation (Mann–Whitney exact test:  $U = 8$ ,  $n_{\text{color}} = 4$ ,  $n_{\text{chance}} = 4$ ,  $P = 1.000$ , two-tailed). Furthermore, a nonparametric test revealed a statistical trend concerning the direct difference in opening preferences between subjects from the weight group and subjects from the color group (Mann–Whitney exact test:  $U = 1$ ,  $n_{\text{weight}} = 4$ ,  $n_{\text{color}} = 4$ ,  $P = 0.057$ , two-tailed). On average, subjects from the weight group opened the juice bottle earlier than subjects from the color group did (average opening position: weight = 1.9, color = 2.9).

After the first testing block, conditions were swapped between groups, which allowed a within-subject comparison. A nonparametric test revealed a significant difference between chance and subjects' opening preferences in the weight condition (Wilcoxon exact test:  $T_+ = 8$ ,  $n = 8$ ,  $P = 0.008$ , two-tailed) but not between chance and their opening preference in the color condition (Wilcoxon exact test:  $T_+ = 3$ ,  $n = 8$ ,  $P = 0.781$ , two-tailed). Furthermore, subjects' opening preference in the weight condition differed significantly from their opening preferences in the color condition (Wilcoxon exact test:  $T_+ = 8$ ,  $n = 8$ ,  $P = 0.008$ , two-tailed). All subjects who received the color condition second (Group 1) opened the juice bottle in that condition later than in the previous weight condition (average opening position: weight = 1.9, color = 3.1), whereas subjects who received the weight condition second (Group 2) opened the juice bottle in that condition earlier than in the previous color condition (average opening position: color = 2.9, weight = 1.7; see Fig. 2).

Over the course of the experiment, subjects' performance improved remarkably during the 15 trials of the weight condition, but did not change during the 15 trials of the color condition (see Fig. 3). In the weight condition,

<sup>2</sup>The colored part covered circa 1/3 of the bottle's surface.



**Fig. 3** Average opening order of the target bottle across all individuals in Experiment 1. *Gray circles* represent subject's performance in the color condition (arbitrary cue), *black squares* represent the performance in the weight condition (causal cue) for each trial. The *dashed line* indicates a random opening order

subjects opened the juice bottle on average at position 2.4 at the beginning (trial 1–5) and at position 1.2 at the end of the testing block (trial 11–15). In the color condition, subjects opened the juice bottle on average at position 2.7 at the beginning and at position 3.3 at the end of the testing block. A nonparametric comparison of subjects' performances during the first five testing trials with their performances during the last five testing trials revealed a significant improvement over time in the weight condition (Wilcoxon exact test:  $T_+ = 8$ ,  $n = 8$ ,  $P = 0.008$ , two-tailed) but not in the color condition (Wilcoxon exact test:  $T_+ = 5$ ,  $n = 8$ ,  $P = 0.195$ , two-tailed).

Both the between-subject and the within-subject comparison suggest that subjects manipulated and finally opened the target bottle significantly earlier when a causal cue (weight) indicated the content of the bottles, whereas their opening behavior was not different from chance when an arbitrary cue (color) was the only information available. Although immediate learning took place in the *causal condition*, the same individuals were not able to benefit from their 15-trials experience in the *arbitrary condition*.

## Experiment 2: exchange paradigm

### Materials and methods

#### Subjects

We tested seven socially housed chimpanzees (three males, four females) with ages between 11 and 34 years (mean = 24.50, SD = 10.28) at the Wolfgang Köhler Primate Research Center in Leipzig–Zoo (Germany). Their group had access to indoor and outdoor areas. All subjects

that participated in that study were tested individually and were never deprived of food or water.

#### Materials

Five identical and opaque 500-ml plastic Coca-Cola bottles served as stimuli—equivalent to the ones used in Experiment 1. The bottles were filled with gypsum (weight = 570 g), or left empty (weight = 70 g), depending on the experimental condition. In the weight condition, all five bottles were visually indistinguishable (entirely gray) but differed in their weight. One bottle weighted 570 g (target) and four bottles weighted 70 g (nontargets). In the color condition, all five bottles weighed 570 g but the lower part of the bottles was colored differently. One bottle was labeled with a white mark (target) and four bottles were labeled with a black mark (nontargets). Prior to the test, all bottles were placed in an opaque plastic repository that covered the bottom part of each bottle (see Fig. 1). This made the salience of the cues in the two test conditions more comparable because subjects could not see or feel any difference between the five bottles until they lifted them.

#### Procedure

The experiment was conducted within the framework of an exchange paradigm (Hyatt and Hopkins 1998) in which subjects had to exchange objects with a human experimenter. There was no need for initial exchange training because all subjects had previous experience in exchanging objects with their keepers.<sup>3</sup> Subjects were required to return objects with a certain feature to the experimenter to obtain a food reward (see Pelé et al. 2009; Schrauf et al. 2009 for a similar method with different species). The experimenter sat outside the cage facing the subject. In order to avoid inadvertent cueing E was looking down while the subject was selecting the objects.

**Pretest** Prior to the test, we assessed whether chimpanzees preferred juice when given the choice between (a) the same amount of juice and water, or (b) juice and nothing/air. The procedure was identical to the one used in Experiment 1.<sup>4</sup>

**Test** Outside of the subject view, the experimenter (E) placed all five bottles in a repository inside an empty

<sup>3</sup> This exchange experience did not involve any differential reinforcement based on the weight or the color of objects. Instead, subjects were required to return objects (e.g., a pen or a piece of paper) that were "stolen" before regardless of particular physical properties.

<sup>4</sup> All seven subjects easily met the criteria and preferred the juice to the alternative bottle (water or empty) in 100% of the cases.

testing room, with the position of the target bottle randomized and counterbalanced across trials.

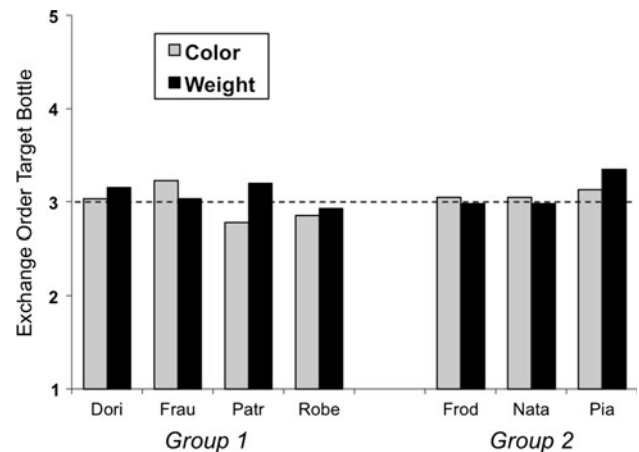
After the subject had entered the testing room, E “asked” for exchange by extending her hand toward an opening in the plexi-glass panel plus repeated (standardized) verbal encouragement. If a subject returned the target object in the weight condition (heavy bottle) she received 50 ml of juice. Whenever a subject returned one of the nontarget objects (light bottle) she received nothing. If a subject returned the target object in the color condition (white bottle) she received 50 ml of juice. Whenever a subject returned one of the nontarget objects (black bottle) she received 50 ml of water. All rewards were given through the exchange opening immediately after the object transfer. We coded the order in which the subject handed the bottles to E. Mere bottle handling (e.g., lifting) without exchange was not scored as a response.

Subjects received both conditions successively (40 trials per condition) with the order of presentation counterbalanced across subjects. Group 1 (four subjects) started with 40 trials of the weight condition followed by 40 trials of the color condition, whereas group 2 (three subjects) received them in the opposite order. All subjects received four trials per day, resulting in 10 testing days per condition and 20 testing days in total. There was at least a 1-day break before conditions were swapped. All data were collected between October and November 2010.

## Results

If subjects treated the bottles randomly, the target bottle should be exchanged third on average. Within the first testing block (trial 1–40), subjects exchange performance did not differ from what would be expected by chance, neither for the weight condition in group 1 (Mann–Whitney exact test:  $U = 4$ ,  $n_{\text{weight}} = 4$ ,  $n_{\text{chance}} = 4$ ,  $P = 0.314$ , two-tailed) nor for the color condition in group 2 (Mann–Whitney exact test:  $U = 0$ ,  $n_{\text{weight}} = 3$ ,  $n_{\text{chance}} = 3$ ,  $P = 0.100$ , two-tailed). In addition, no performance differences between the two testing groups could be found (Mann–Whitney exact test:  $U = 6$ ,  $n_{\text{weight}} = 4$ ,  $n_{\text{color}} = 3$ ,  $P = 1.00$ , two-tailed; average exchange position: weight = 3.1, color = 3.1).

After the first testing block, conditions were swapped between groups, which allowed us to conduct a within-subject comparison. A nonparametric test revealed no difference between chance and subjects’ exchange performance, neither in the weight condition (Wilcoxon exact test:  $T_+ = 2$ ,  $n = 7$ ,  $P = 0.125$ , two-tailed) nor in the color condition (Wilcoxon exact test:  $T_+ = 2$ ,  $n = 7$ ,  $P = 0.750$ , two-tailed). Furthermore, no differences in subjects’ exchange performance were found between the weight and the color condition (Wilcoxon exact test:  $T_+ = 8$ ,  $n = 8$ ,  $P = 0.188$ , two-tailed). In other words, subjects who received the color



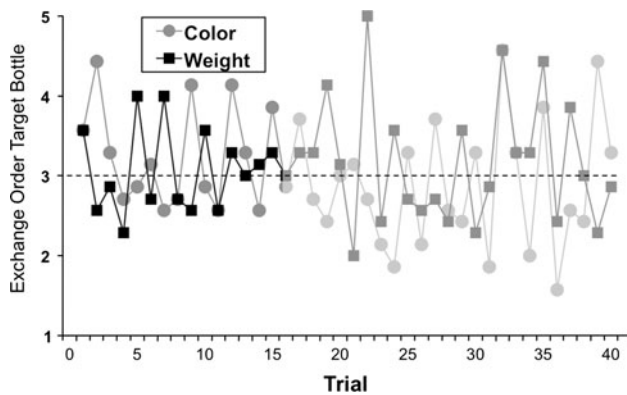
**Fig. 4** Average exchange order of the target bottle for each individual across all 40 trials of Experiment 2. *Gray bars* represent subject’s performance in the color condition (*white target*); *black bars* represent the performance in the weight condition (*heavy target*). The *dashed line* indicates a random exchange order

condition second (Group 1) did not change their exchange behavior in comparison to the previous weight condition (average exchange position: weight = 3.1, color = 3.0), and subjects who received the weight condition second (Group 2) did not change their exchange behavior in comparison to the previous color condition (average exchange position: color = 3.1, weight = 3.2; see Fig. 4).

Over the course of the experiment, subjects’ performance did not improve (or degrade) in neither of the two conditions (see Fig. 5). In the weight condition, subjects exchanged the target bottle on average at position 3.1 at the beginning (trial 1–10) and at position 3.3 at the end of the testing block (trial 31–40). In the color condition, subjects exchanged the target bottle at average on position 3.2 at the beginning and at position 3.0 at the end of the testing block. A nonparametric comparison of subjects’ performances during the first ten testing trials with their performances during the last ten testing trials revealed no significant change over time, neither in the weight condition (Wilcoxon exact test:  $T_+ = 5$ ,  $n = 7$ ,  $P = 0.313$ , two-tailed) nor in the color condition (Wilcoxon exact test:  $T_+ = 2$ ,  $n = 7$ ,  $P = 0.297$ , two-tailed). Both the between-subject and the within-subject comparison suggest that subjects exchange behavior as well as their learning speed were not influenced by the nature of the target cue given (weight or color).

## Discussion

During their first few exposures to the problem in Experiment 1, all subjects opened the bottles indiscriminately in both conditions. In the weight condition, subjects rapidly learned to open the heavy bottle before the light bottles, but the same individuals were not able to learn an association



**Fig. 5** Average opening order of the juice bottle across all individuals in Experiment 2. *Gray circles* represent subject's performance in the color condition (*white target*), *black squares* represent the performance in the weight condition (*heavy target*) for each trial. The *dashed line* indicates a random opening order. The first 15 trials are highlighted to facilitate a comparison with the data from Experiment 1

between color and reward during the course of the experiment (15 trials). It is important to remember that in the given scenario, both types of cues—causal and arbitrary—statistically provided the same predictive value, because the cue–outcome relation was totally reliable in both cases. Nevertheless, chimpanzees found the target bottle faster when the cue and the reward bore a causal relation than when they simply reflected an arbitrary regularity.

Could it be that some kinds of cues (e.g., weight) per se imply a higher predictive value toward a possible outcome than others? We do not think the physical feature itself induces that difference (e.g., that weight is always more salient than color). Instead, we suggest that it strongly depends on the context in which cues are and are not preferably used by animals. Results of Experiment 2 support this view. In stark contrast to Experiment 1, no predominance of the feature *weight* over *color* could be identified when explicitly providing a noncausal context in which both weight and color cues were presented as arbitrary features. In an entirely arbitrary exchange setting, weight and color cues seemed equally easy or hard to learn for the tested chimpanzees (Experiment 2), a result that exactly resembles previous data obtained from bonobos, gorillas, and orangutans (Schrauf et al. 2009). In a very similar setup to the one presented here, subjects learned the color discrimination even slightly faster than the weight discrimination. The crucial similarity between the Schrauf and Call (2009) and Experiment 2 of the current study is that in the given context, neither of the cues was of a compulsory causal nature; hence, there was no reason to prefer one cue to the other. Moreover, Schrauf and Call (2011) found that apes quickly learned to locate a hidden reward in one of two identical containers that only differed in their weight. In contrast, apes were unable to solve the same task when they

had to use the color and patterns printed on the containers. This result confirms and reinforces our current findings with a different paradigm.

On the basis of previous and current data, we postulate that chimpanzees (and probably other animals as well) assess causally structured stimulus relations in a fundamentally different way than when assessing purely arbitrary stimulus associations. In other words, chimpanzees' cognitive systems seem naturally built to benefit from causal structures; when confronted with problems containing purely arbitrary relations, they have to rely on a costly general learning mechanism. Even though associative learning theory has enhanced and reconsidered its premises during the last decades (Rescorla and Wagner 1972; Van Hamme and Wasserman 1994) it has yet to explain satisfactorily why the predictive power of certain stimulus associations is so context dependent (see also Waldmann and Hagmayer 2005 for a related discussion).

In the following, we address some potential points of methodological criticism concerning Experiment 1. Given that during the preparation phase, the first bottle on the left was always filled with juice and the other four were either left empty (weight condition) or filled with water (color condition), the question arises as to whether this procedural characteristic somehow influenced subjects' opening behavior in the subsequent manipulation phase. Our data suggest that it did not. In the *causal condition*, subjects did not show any obvious opening preference based on the bottle's location within the repository. Apparently, their manipulative behavior was guided by causal reasoning rather than a simple sequential "one-after-the-other" searching approach. In the *arbitrary condition*, subjects seemed to prefer to manipulate the bottles in a serial fashion—starting in the repository either with bottle 1 (far left) or with bottle 5 (far right). However, in spite of having always seen bottle 1 filled with juice in the preparation phase, subjects seemed to prefer to start manipulating bottle 5 (41% of all cases) rather than bottle 1 (29% of all cases). This suggests that they did not transfer any information about bottle position from the preparation phase to the manipulation phase.

Some may wonder why chimpanzees could not learn the given color–reward association in the *arbitrary condition* of Experiment 1, and furthermore that they could not learn the arbitrary relation between color or weight and a reward in the exchange setting of Experiment 2. The fact that subjects failed to learn this arbitrary regularity during the 15 trials in Experiment 1 and during the 40 trials in Experiment 2 is not surprising and fits with previous data (e.g., Call 2006b; Hanus et al. 2008). Chimpanzees certainly have the capacity to learn such arbitrary continuities—when given (much) more training. Grasping the causal logic of the given problem on the other hand seemed comparatively easy for our subjects.

Where this “preparedness” for causal inferences derives from remains an open question. On the basis of the current data, we cannot determine whether or not this is an inherent ability, like some kind of core knowledge (e.g., Carey and Spelke 1996), or whether it is a purely learned competence (e.g., Dickinson and Shanks 1985; Heyes and Dickinson 1990). Perhaps both components are important. Recurrent experience during ontogeny definitely plays an important role in the acquisition of such cognitive skills—in human and nonhuman primates alike. Individuals need to interact repeatedly with various causal regularities within their physical world in order to be capable of transferring this specific knowledge to new situations. Such cognitive transfer is essential for dealing more efficiently with future problems (Waldmann et al. 2006). In addition, it seems plausible from an evolutionary perspective that animals facing a complex and quickly changing environment would profit from a cognitive predisposition that enables them to learn causal relations more quickly and readily than any other kind of stimulus associations.

**Acknowledgments** We are extremely grateful to the management, the trustees and especially the staff of the Ngamba Island Chimpanzee Sanctuary for their help and support. We also appreciate permission from the Ugandan National Council for Science and Technology and the Uganda Wildlife Authority. Special thanks go to Katja Karg for her help with the data collection, to the keepers of the zoo Leipzig, and to Raik Pieszek for his help in constructing the experimental apparatus.

## References

- Call J (2004) Inferences about the location of food in the great apes (*Pan paniscus*, *Pan troglodytes*, *Gorilla gorilla*, and *Pongo pygmaeus*). *J Comp Psychol* 118:232–241
- Call J (2006a) Descartes’ two errors: reason and reflection in the great apes. In: Hurley S, Nudds M (eds) *Rational animals?*. Oxford University Press, Oxford, pp 219–234
- Call J (2006b) Inferences by Exclusion in the great apes: the effect of age and species. *Anim Cogn* 9:393–403
- Carey S, Spelke E (1996) Science and core knowledge. *Philos Sci* 63:515–533
- Dickinson A, Shanks D (1985) Animal conditioning and human causality judgment perspectives on learning and memory. Lawrence Erlbaum Associates, Inc, Hillsdale, pp 167–191
- Hanus D, Call J (2008) Chimpanzees infer the location of a reward on the basis of the effect of its weight. *Curr Biol* 18:R370–R372
- Heyes C, Dickinson A (1990) The intentionality of animal action. *Mind Lang* 5:87–103
- Hyatt CW, Hopkins WD (1998) Interspecies object exchange: bartering in apes? *Behav Process* 42:177–187
- Krebs JR, Davies NB, Parr J (1993) An introduction to behavioural ecology, 3rd edn. Blackwell Scientific Publications, Cambridge
- Martin-Ordas G, Call J (2009) Assessing generalization within and between trap tasks in the great apes. *Int J Comp Psychol* 22:43–60
- McFarland D (1993) Animal behaviour: psychobiology, ethology, and evolution, 2nd edn. Longman Scientific & Technical, Longman Group UK Ltd/Wiley, Harlow/New York
- Pelé M, Dufour V, Thierry B, Call J (2009) Token transfers among great apes (*Gorilla gorilla*, *Pongo pygmaeus*, *Pan paniscus*, and *Pan troglodytes*): species differences, gestural requests, and reciprocal exchange. *J Comp Psychol* 123:375–384
- Rescorla RA, Wagner AW (1972) A theory of Pavlovian conditioning: variations in the effectiveness of reinforcement and nonreinforcement. In: Black AH, Prokasy WF (eds) *Classical conditioning II: current research and theory*. Appleton-Century-Crofts, USA, pp 64–99
- Schrauf C, Call J (2009) Great apes’ performance in discriminating weight and achromatic color. *Anim Cogn* 12:567–574
- Schrauf C, Call J (2011) Great apes use weight as a cue to find hidden food. *Am J Primatol* 73:323–334
- Van Hamme LJ, Wasserman EA (1994) Cue competition in causality judgments: the role of nonpresentation of compound stimulus elements. *Learn Motiv* 25:127–151
- Visalberghi E, Néel C (2003) Tufted capuchins (*Cebus apella*) use weight and sound to choose between full and empty nuts. *Ecol Psychol* 15:215–228
- Waldmann MR, Hagmayer Y (2005) Seeing versus doing: two modes of accessing causal knowledge. *J Exp Psychol Learn Mem Cogn* 31:216–227
- Waldmann MR, Hagmayer Y, Blaisdell AP (2006) Beyond the information given: causal models in learning and reasoning. *Curr Dir Psychol Sci* 15:307–311