

Great Apes (*Pan paniscus*, *Pan troglodytes*, *Gorilla gorilla*, *Pongo abelii*) Follow Visual Trails to Locate Hidden Food

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Whether nonhuman primates understand causal relations beyond mere associations is still a matter of debate. We presented all four species of nonhuman great apes ($N = 36$) with a choice between 2 opaque, upside down cups after displacing them out of sight from their starting positions. Crucially, 1 of them had left a yogurt trail behind it. Great apes spontaneously used the trail to select the yogurt baited cup. Follow-up experiments demonstrated that chimpanzees distinguished trails based on the temporal order of cause and effect by ignoring trails that were already present before the reward was hidden. Additionally, chimpanzees did not select cups based on the amount of yogurt near them but instead preferred cups that signaled the endpoint of the trail. We conclude that apes' choices reveal sensitivity to a causal relation between cause (reward) and effect (trail) including their temporal order.

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Stepping outside the house on a winter morning, we see a fresh snow cover with a single track of footprints leading down the alley. Without observing the cause of the tracks we immediately infer that someone has already walked down the alley this morning. Moreover, based on the shape of the footprints we infer that the cause of the track was a human and not some kind of animal.

Humans routinely make this kind of causal inference taking into account the spatiotemporal order of cause and effect. In fact, diagnostic causal reasoning is well documented in adult humans (e.g., Waldmann, 2000, 2001) and children as young as 2–4 years of age (e.g., Gopnik, Sobel, Schulz, & Glymour, 2001). The extent to which nonhuman animals are also capable of performing such causal diagnosis going beyond mere associations is a crucial issue and subject of an ongoing debate (Blaisdell & Waldmann, 2012; Penn & Povinelli, 2007; Seed & Call, 2009; Visalberghi & Tomasello, 1998). This debate centers on the question whether or not nonhuman animals are capable of representing unobservable causal mechanisms and structures.

Two main types of relations have so far been used to shed light on diagnostic reasoning in nonhuman animals: object–object relations and spatiotemporal relations. First of all, object–object relations have been examined using folk physics paradigms including among others the investigation of support (Call, 2007; Schloegl, Waldmann, & Fischer, 2013), weight (Hanus & Call, 2008, 2011; Povinelli, 2011; Schrauf & Call, 2011), and connectivity (Albiach-Serrano, Bugnyar, & Call, 2012; Cacchione & Call, 2010; Herrmann, Wobber, & Call, 2008; Povinelli, Reaux, Theali, & Giambrone, 2000). In these studies, subjects had to use knowledge about object–object relations either to avoid obstacles or to infer food locations. However, the question remains whether animals differentiate between mere covariation and causal relations (Blaisdell & Waldmann, 2012). Spatiotemporal relations between events instantiated either as arbitrary or natural causality perhaps offer us a better suited approach than object–object relations to resolve this issue.

Arbitrary causality (also *weak* causality, *sensu* Kummer, 1995; Hume, 1978; Premack & Premack, 1994) refers to associatively learned events. For instance, Blaisdell et al. (2006) found evidence that rats (*Rattus norvegicus*) do form causal representations that integrate and distinguish events merely based on observations and events the rats caused by means of their own interventions. Importantly, this approach did not require any physical knowledge but depended on classical and operant preconditioning. Natural causality (also *strong* causality, *sensu* Kummer, 1995; Premack & Premack, 1994), in contrast, focuses on special, naturalistic pairings of events and does not rely on learning. For example, Premack and Premack (1994) showed chimpanzees how an experimenter hid an apple and a banana in two different containers. The ape's view to the containers was then occluded. What the chimpanzee saw next was the experimenter eating one of the two fruits. The chimpanzee could now choose between the two containers. One of

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four chimpanzees decided consistently for the container with the fruit different from the one eaten by the experimenter. Thus, Premack and Premack concluded, this chimpanzee might have inferred that the experimenter had removed one of the fruits from the container out of her sight. Therefore, the container associated with the fruit eaten by the experimenter would not contain a piece of fruit any more. Since then, several studies have produced positive evidence for such diagnostic inference by exclusion in nonhuman primates (Call, 2004, 2006b; Hill, Collier-Baker, & Suddendorf, 2011; Sabbatini & Visalberghi, 2008).

In the present study, we examined nonhuman great apes' causal knowledge by combining information about object-object and spatiotemporal relations, while minimizing the physical knowledge needed. We presented apes with a choice between two upside down opaque cups after displacing them from their starting positions. One of the cups had a yogurt trail behind it. Like a human tracking footprints in the snow, we expected that if the apes understood the significance of the trail, they would follow it to the baited cup. Crucially, causal knowledge but not associative knowledge makes predictions in such situations with regard to (a) the temporal directionality of cause and effect, and (b) the logico-causal relation between two spatiotemporally coupled events (Blaisdell & Waldmann, 2012). First of all, a cause A produces an effect B and not vice versa. An association between events A and B, in contrast, implies no directionality. In the present task, causal knowledge but not associative knowledge would allow the apes to infer that the hidden displacement of the reward had generated the trail. Thus, trails that existed before the reward had been hidden could not have been an effect of the object displacement. Second, causal knowledge helps us to distinguish between mere covariation and causation. In the current set-up, causal knowledge entails an understanding that only displacing yogurt will produce a yogurt trail (but not the displacement of other types of food). In associative learning the learning rate of two covarying events A and B should be the same irrespective of whether they are logico-causally related or not. Thus, with a purely associative learning mechanism at work, it should not matter whether the yogurt trail was associated with the location of a yogurt bowl or the location of a dry food pellet.

In the context of such secondary cues, children as young as 2.5 years of age (but not younger ones) used the tracks in a sandbox to locate a hidden toy, particularly when alerted that the tracks indicated the location of the toy (Sodian, Taylor, Harris, & Perner, 1991). In nonhuman primates there is hardly any evidence for the usage of such indirect cues in the wild (e.g., snake tracks or carcasses, Cheney & Seyfarth, 1990), with the exception of reports about chimpanzees reacting aggressively toward nests of other chimpanzee groups (Goodall et al., 1979) and about chimpanzees detecting invisible underground bee hives based on the small wax entrance to the hive (Boesch, Head, & Robbins, 2009). Besides, there are some anecdotes about brown bears (*Ursus arctos*) tracking human footprints in the wild (described in Burghardt, 1992). However, whether these behaviors are based on any kind of causal inference remains unclear. Of course there have been also reports about other nonhuman animals following (mostly chemical) trails such as ants (e.g., Harrison, Fewell, Stiller, & Breed, 1989) or

blind snakes (e.g., *Ramphotyphlops nigrescens*, Webb & Shine, 1992). It is unlikely, however, that these examples involve causal inferences but rather innate behavioral rules.

Experiment 1 examined whether apes would follow a yogurt trail to locate a yogurt bowl (causal condition) or a dry food pellet (arbitrary condition). Moreover, we investigated whether the apes needed to see how the trails were produced in the first place in order to use the trails as a cue. Therefore, we compared subjects that started with trials in which they could see how one of the two opaque cups produced a trail with subjects that had to infer the location of the reward retrospectively based on the trail.

Experiment 1

Materials and Method

Subjects. Fourteen chimpanzees (*Pan troglodytes*), five orangutans (*Pongo abelii*), seven bonobos (*Pan paniscus*), and four gorillas (*Gorilla gorilla*) participated in this experiment. The subjects were housed at the Wolfgang Köhler Research Centre, Leipzig Zoo (Leipzig, Germany). Two of the 14 chimpanzees stopped approaching the testing site after a few sessions and were therefore excluded from data analysis except for the first trial analysis. Our final sample consisted of 19 females and nine males aged between 7 and 37 years (M_{age} 18.6 years, see Table S1 for detailed information on each subject). Subjects had participated in various cognitive tasks prior to the study including object displacement tasks (none involving trails though). Four of 12 chimpanzees had previous experience with trails in Pilot Experiments 1 and 2 in which they failed to follow the trails (see online supplementary material).

Procedure and design. Subjects were tested individually. The experimenter (E) sat behind the sliding platform (78 cm × 35 cm) facing the subject who was behind a transparent acrylic glass panel. This panel contained two or three horizontally aligned, circular holes (6 cm). At the beginning of each trial E slid the platform back and placed a sheet of brown paper (50 cm × 25 cm) on the sliding table. Then he placed two red cups (8.5 cm × 8.5 cm) on top of the brown paper with the open side facing the apes. The cups were located near the edge of the platform closest to E. We varied two factors between our subjects: the type of reward (causal vs. arbitrary condition) and the type of information the subjects received at first (see first vs. infer first). In the causal condition, a white yogurt bowl was placed centrally between the two red cups and a spoonful of strawberry or cherry yogurt was poured into the yogurt bowl in full view of the subject. In trials in which a trail was made this yogurt bowl contained a triangular hole in the bottom (2 cm × 2 cm × 1 cm). In the arbitrary condition, a banana pellet was placed between the two opaque cups.

There were three different trial types depending on the information given to the subjects: see, infer, and control (see Figure 1 a–c). In “see” trials, E placed an opaque screen in-between the subject and the sliding table to occlude the subjects' view. Then E hid the yogurt bowl/banana pellet under one of the red cups. Subsequently, E removed the screen and the subjects got visual access to the platform and the two cups, both now with the open side facing down. E then moved the two cups simultaneously across the brown paper toward the left and right hole in the Plexiglas panel, respectively. Crucially, in the causal condition the cup with the yogurt

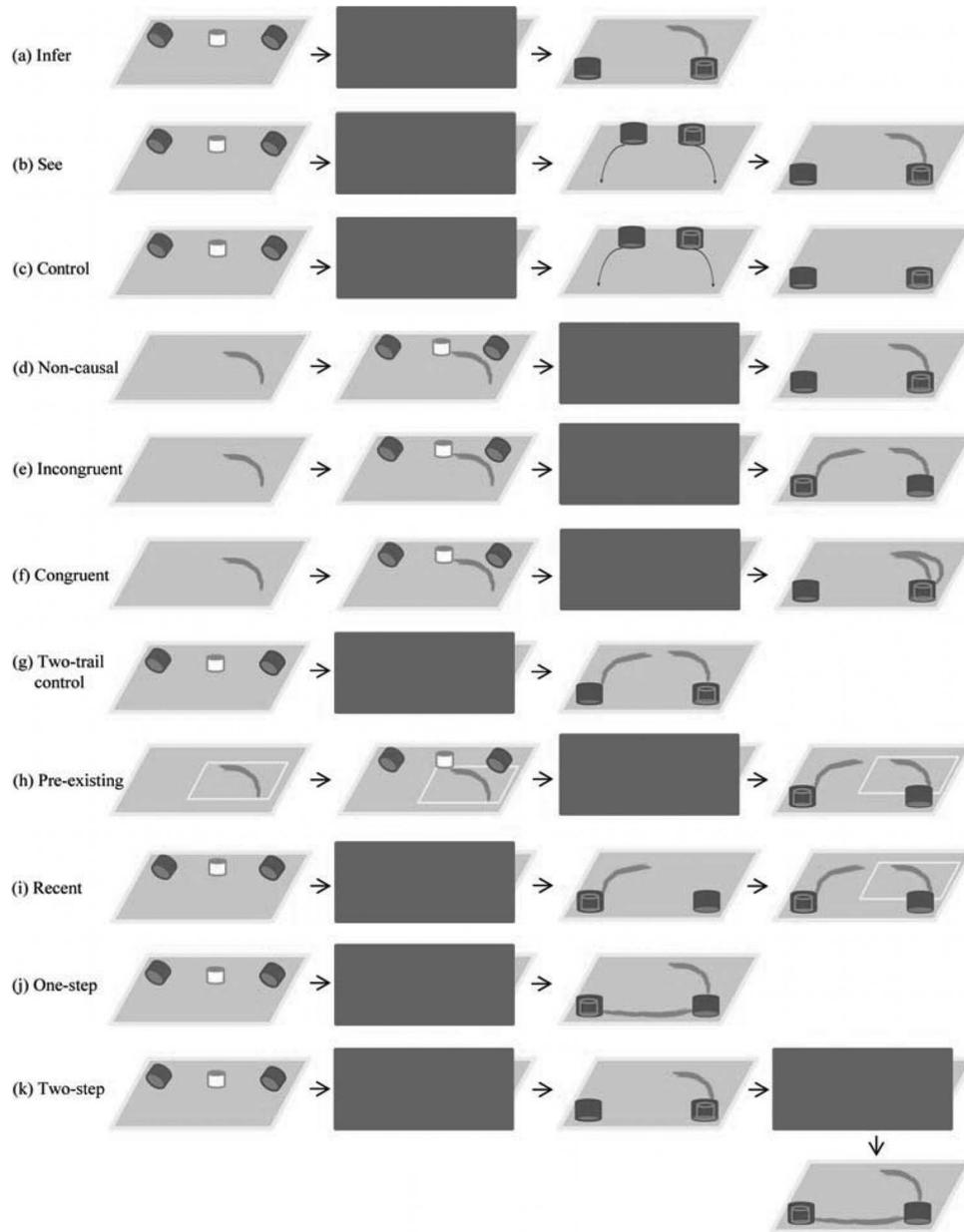


Figure 1. Illustration depicting the course of all trial types conducted throughout the current study (as shown from perspective of the subjects). After the last image in the sequence of each trial type, subjects were allowed to pick one of the two opaque cups. The black arrows in (b) and (c) indicate that the displacement of the cups took place in full view of the subject. Experiment 1 (causal condition): (a) infer, (b) see, and (c) control trials; Experiment 2: (a) infer, (c) control, and (d) noncausal trials; Experiment 3: (e) incongruent, (f) congruent, and (g) two-trail control trials; Experiment 4: (h) preexisting and (i) recent trials; Experiment 5: (a) infer, (j) one-step, and (k) two-step trials.

bowl underneath produced a salient yogurt trail while being moved across the paper in full view of the subject. In the arbitrary condition the baited cup did not produce a trail; however, E produced an identical yogurt trail leading to the baited cup by means of a spoon as soon as the cups were in their final position.

In “infer” trials, the only difference to the “see” trials was that the occluding screen stayed in place until the two cups had been

displaced across the sheet of paper and the trails were produced. That is, in infer trials the subjects had to infer from the presence of the trail where the yogurt/pellet had been hidden.

In “control” trials, the difference to the “see” trials was that the yogurt bowl in the causal condition did not contain a hole in the bottom and therefore did not produce a trail while being moved across the paper. In the arbitrary condition, no trail was produced

either. Thus, the apes got no obvious cue where the yogurt was located in these control trials.

After the cups had been displaced across the sheet of paper (and the screen had been removed in the infer condition) E pushed the platform forward to allow subjects to choose one of the options. The cups were now in front of the left and right hole in the panel, respectively, and subjects could make their choice by sticking their fingers through one of the holes.

E turned over the cup that was selected by the ape. In a few trials apes' selection was equivocal (i.e., apes selected both cups simultaneously or switched rapidly between the two). In those cases E pushed the platform back and forth again until the subject made an unambiguous decision, something that occurred only in a small subset of trials. If the subject chose the correct cup she received a spoonful of yogurt from the yogurt cup or the banana pellet depending on the causal/arbitrary condition. Importantly, the apes never received the yogurt that made up the trials. If the subject chose the incorrect cup, E removed the yogurt bowl/pellet without rewarding the subject. Then E started the next trial by sliding back the platform and placing a new sheet of brown paper on the table.

We divided our subjects into two groups according to the order in which they received the trial types. The see-first group received the see condition in the first three sessions and the infer condition in the last three sessions. The infer-first group received first the infer condition and then the see condition. All subjects with the exception of four chimpanzees who had prior experience with trials (see Pilot Experiments 1 and 2) were then further subdivided into a causal and arbitrary group. The four experienced chimpanzees received the causal condition too. The causal group received yogurt as reward, whereas the arbitrary group got banana pellets instead of yogurt. We assigned naïve subjects to the groups randomly except that we balanced the groups for age, sex, and species as much as possible (causal group: nine females, three males, 16.3 years; arbitrary group: seven females, five males, 16.8 years).

We administered 12 trials per session, each including eight trials of the infer and see condition, respectively, and four trials of the control condition. In half of the trials the reward was moved to the left and to the right, respectively. We pseudorandomized the order of trials within a session with the restriction that no more than three consecutive trials were to same direction and no more than four consecutive trials were of the same condition. All subjects completed six sessions, for a total of 24 trials per condition.

Scoring and analysis. We videotaped all sessions. We scored the first choice of the subjects after E had pushed the sliding table to the subject. A second coder scored 20% of all trials to assess interobserver reliability which was excellent ($K = 0.95$, $N = 408$, $p < .001$).

On a group level, we used the Friedman test to compare different trial types followed by Wilcoxon signed-ranks test for post hoc pairwise comparisons between trial types (using Holm-Bonferroni correction to account for multiple comparisons). In addition, we used the Wilcoxon's test to test against the chance level ($p = .5$). To compare groups of subjects (arbitrary vs. causal group, see-first vs. infer-first group, naïve vs. experienced subjects) we employed the Mann-Whitney U test. To compare performance across species we used the Kruskal-

Wallis H-test. For the first trial analysis of each subject and individual data we conducted binomial tests against the chance value ($p = .5$). All p values reported here are exact and two-tailed.

Results and Discussion

We found no significant difference between naïve and experienced chimpanzees (causal condition only) in any of the trial types (see: $U = 6.5$, $N_1 = 4$, $N_2 = 4$, $p > .5$; infer: $U = 3.5$, $N_1 = 4$, $N_2 = 4$, $p > .1$; control: $U = 3.0$, $N_1 = 4$, $N_2 = 4$, $p > .1$). Therefore, we pooled subjects regardless of experience in subsequent analyses. Additionally, we found no significant effect of species in any of the trial types (see: $\chi^2 = 2.79$, $df = 3$, $p > .1$; infer: $\chi^2 = 2.99$, $df = 3$, $p > .1$, $p > .1$; control: $\chi^2 = 1.21$, $df = 3$, $p > .5$). Therefore, we collapsed data also across species. Moreover, we found no significant order effect between subjects that started with the infer condition or with the see condition neither in the causal (see: $U = 30$, $N_1 = 8$, $N_2 = 8$, $p > .5$; infer: $U = 18.5$, $N_1 = 8$, $N_2 = 8$, $p > .1$; control: $U = 16.5$, $N_1 = 8$, $N_2 = 8$, $p > .1$) nor in the arbitrary condition (see: $U = 17$, $N_1 = 6$, $N_2 = 6$, $p > .5$; infer: $U = 17$, $N_1 = 6$, $N_2 = 6$, $p > .5$; control: $U = 14$, $N_1 = 6$, $N_2 = 6$, $p > .5$). Therefore, we collapsed trials across the order of presentation.

There was a significant effect of trial type in the causal condition ($F = 10.07$, $N = 16$, $df = 2$, $p < .01$) but not in the arbitrary condition ($F = 2.93$, $N = 12$, $df = 2$, $p > .1$). Pairwise comparisons between trial types in the causal condition revealed that subjects performed significantly better in see ($T^+ = 101.5$, $N = 15$, $p < .05$) and infer trials ($T^+ = 122.5$, $N = 16$, $p < .01$) compared with control trials. In contrast, no significant difference was found between infer and see trials of the causal condition ($T^+ = 81.5$, $N = 14$, $p = .07$). Additionally, we found that the apes in the causal condition scored significantly above chance in see ($65.1 \pm 3.5\%$ correct, $T^+ = 101.5$, $N = 14$, $p < .001$) and infer trials ($73.2 \pm 3.9\%$ correct, $T^+ = 136$, $N = 16$, $p < .001$) but not in control trials ($48.7 \pm 3.2\%$ correct, $T^+ = 66$, $N = 15$, $p > .5$; see Figure 2a). In contrast, apes in the arbitrary condition performed at chance levels in all trial types (see: $50.0 \pm 2.2\%$ correct, $T^+ = 23$, $N = 9$, $p = 1$; infer: $54.2 \pm 2.2\%$ correct, $T^+ = 43$, $N = 10$, $p > .1$; control: $48.6 \pm 1.6\%$ correct, $T^+ = 24$, $N = 8$, $p > .1$).

Comparing the causal and arbitrary condition, we found that subjects in the causal condition outperformed subjects in the arbitrary condition in see ($U = 32.5$, $N_1 = 16$, $N_2 = 12$, $p < .01$) and infer trials ($U = 22$, $N_1 = 16$, $N_2 = 12$, $p < .001$) but not in control trials ($U = 105.5$, $N_1 = 16$, $N_2 = 12$, $p > .5$).

Finally, to rule out learning effects over the course of the experiment, we analyzed apes' first trial performance which revealed that subjects in the causal condition (but not in the arbitrary condition) scored significantly above chance already in their very first trial involving a trial (infer or see trials depending on the order of presentation; causal condition: 15 of 18 correct, 83.3%, binomial test: $p < .01$; arbitrary condition: six of 12 correct, 50.0%, binomial test: $p = 1.0$).

At the individual level, four apes scored significantly above chance (binomial test: $p < .05$) in see trials (two chimpanzees and two bonobos) and seven apes in infer trials (two chimpanzees, four bonobos, and one orangutan) yet none of the apes

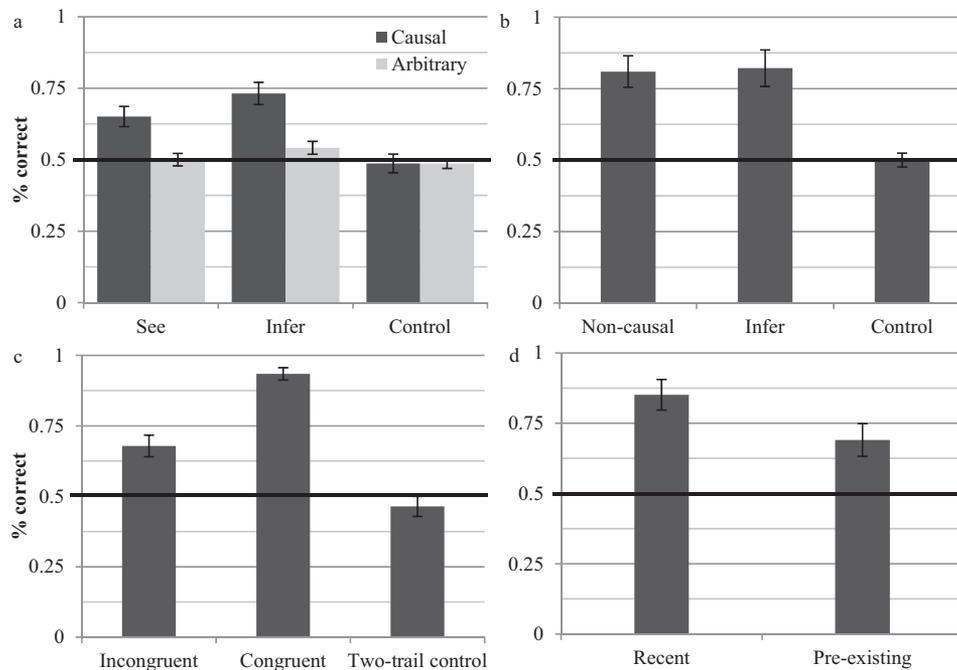


Figure 2. Performance (mean per cent correct \pm SE) as a function of condition (arbitrary vs. causal) and trial type (a). Experiment 1 (N = 28), (b) Experiment 2 (N = 7), (c) Experiment 3 (N = 7), and (d) Experiment 4 (N = 7).

scored better than chance in control trials. All apes that scored significantly above chance were in the causal condition.

These results show that great apes use trails to locate the food but only if the trail and the type of reward are consistent from a causal point of view. One might argue that in the see trials of the arbitrary condition the displacement of the cups and the trail production did not match temporarily (as the trails in the arbitrary condition were only produced after the cups were in their final position) which might in turn explain the difference to the causal condition. However, such an explanation would fail to account for the difference between arbitrary and causal condition in infer trials. Previous experience with other types of trails (Pilot Experiments 1 and 2) or experience with how the trail is produced (see condition) was not necessary for the apes to solve the infer condition. Furthermore, apes' poor performance in control trials make inadvertent experimenter-given cues appear unlikely. Finally, first-trial analysis even indicates that apes spontaneously used the trails in infer trials to locate the food.

We did not find any significant species differences in the current task. However, due to the small sample sizes, this result has to be considered with caution. The individual data showed that some chimpanzees, bonobos, and orangutans at least were able to use the trails to find the hidden yogurt cup. Interestingly, the only species in which none of the tested individuals scored significantly above chance was the gorillas.

One candidate explanation for apes' performance in the current task is that they followed the trails in the causal condition based on the inference that the food had been displaced to one of the cups out of their sight while leaving the trail. Alternatively,

the apes might have decided for the cup that was marked and surrounded by the same type of food as the reward without any causal inference. To differentiate between these two accounts, we presented seven chimpanzees who scored significantly above chance at the individual level in the causal condition of Experiment 1 and Pilot Experiment 3, respectively, with a series of follow-up experiments. Thereby, follow-up Experiments 2–4 examined whether apes took the temporal order of cause and effect into account in the current setting and Experiment 5 investigated whether apes made their choice merely based on the quantity of yogurt surrounding the cups.

Experiment 2

Materials and Method

Subjects. Seven chimpanzees (*Pan troglodytes*) participated in this experiment. There were five females and two males aged between 7 and 36 years (M_{age} 19.1 year, see Table S1).

Procedure and design. There were three trial types: infer, control, and noncausal (see Figure 1a, c, and d). Infer and control trials were identical to Experiment 1 (causal condition). In the noncausal trials E placed a sheet of brown paper on the platform that already exhibited a yogurt trail. These preexisting yogurt trails in noncausal trials were produced in the same way as in infer trials. Then E placed the reward and the two red cups on the platform. E occluded the scenery by means of the screen and hid the yogurt cup under one of the two cups at the endpoint of the preexisting trail (without leaving a second trail). Then he removed the screen again and pushed the platform forward and the subject could make her choice.

We administered 12 trials per session with four trials per condition. In half of the trials the reward was moved to the left and to the right, respectively. We pseudorandomized the order of trials with the restriction that no more than three consecutive trials were to same direction and no more than two consecutive trials were of the same condition. All subjects completed six sessions, for a total of 24 trials per condition.

Scoring and analysis. Same as in Experiment 1.

Results and Discussion

We found a significant effect of trial type ($F = 11.39$, $N = 7$, $df = 2$, $p < .01$). Subjects scored significantly better in infer ($T^+ = 28$, $N = 7$, $p < .05$) and noncausal trials ($T^+ = 28$, $N = 7$, $p < .05$) than in control trials. No significant difference was found between infer and noncausal trials ($T^+ = 9$, $N = 5$, $p > .5$). In line with that, the seven chimpanzees scored significantly above chance in infer ($82.1 \pm 6.4\%$ correct, $T^+ = 28$, $N = 7$, $p < .05$) and noncausal trials ($81.0 \pm 5.5\%$ correct, $T^+ = 28$, $N = 7$, $p < .05$) but not in control trials ($50.0 \pm 2.4\%$ correct, $T^+ = 8$, $N = 5$, $p = 1.0$; see Figure 2b).

Comparing the performance in the first three sessions with the last three sessions we found no significant improvement in any trial type (noncausal: $T^+ = 12$, $N = 5$, $p > .1$; infer: $T^+ = 10$, $N = 4$, $p > .1$; control: $T^+ = 6$, $N = 4$, $p > .5$).

At the individual level, four of seven chimpanzees scored significantly above chance in the noncausal condition and three in the infer condition (binomial test: $p < .05$). None of the apes scored above chance in the control condition.

First of all, these results replicate the findings obtained in Experiment 1 (infer trials). Moreover, these findings suggest that chimpanzees that successfully used the trails in Experiment 1 would also use the trail as hint to locate the reward when the trail had no obvious causal relation with the displacement of the reward. However, note that in the noncausal trials the preexisting trail was the only cue that was available to the apes. Therefore, they might have used the noncausal trail as hint even though they might have understood that it had no causal relation to the reward. Another possibility is that the apes assumed that the baited cup had left a trail which overlapped spatially with the preexisting one. To examine whether the apes could screen off a noncausal (preexisting) trail from a causal trail we ran another follow-up experiment; this time with two trails, one preexisting (noncausal) and a second one made while the reward was hidden (causal).

Experiment 3

Materials and Method

Subjects. Same as in Experiment 2.

Procedure and design. There were three different trial types that all involved two trails: incongruent, congruent, and two-trail control (see Figure 1e–g). In the incongruent and congruent trials, E placed a sheet of brown paper on the platform that already exhibited a yogurt trail. Then E placed the reward and the two red cups on the platform. E occluded the scenery and hid the yogurt bowl under one of the two cups while leaving a second yogurt trail. In congruent trials, he hid

the yogurt bowl under the cup that was marked by the preexisting trail, that is, both trails were leading to the same cup. Nevertheless, both trails were spatially separated and visually distinct. In incongruent trials, E hid the yogurt bowl under the cup that was not marked by the preexisting trail, that is, the trails were symmetrical and leading to different cups. In two-trail control trials, the sheet of brown paper did not exhibit a preexisting trail. When E occluded the scenery he made two, symmetrical trails, one to the baited and one to the nonbaited cup; that is, the apes did not receive any information about which trail was the causal one. Thus, subjects should not have known the location of the reward in these control trials. Then E removed the screen and pushed the platform forward so that the subject could choose between the two cups.

The number of trials per condition and pseudorandomization was identical to Experiment 2.

Scoring and analysis. Same as in Experiment 1.

Results and Discussion

We found a significant effect of trial type ($F = 12.29$, $N = 7$, $df = 2$, $p < .001$). Subjects scored significantly better in congruent than incongruent ($T^+ = 28$, $N = 7$, $p < .05$) and two-trail control trials ($T^+ = 28$, $N = 7$, $p < .05$). Moreover, subjects scored significantly better in incongruent trials than in two-trail control trials ($T^+ = 27$, $N = 7$, $p < .05$). In line with that, the chimpanzees scored significantly above chance in congruent ($93.5 \pm 2.2\%$ correct, $T^+ = 28$, $N = 7$, $p < .05$) and incongruent trials ($67.9 \pm 3.8\%$ correct, $T^+ = 21$, $N = 6$, $p < .05$) but not in two-trail control trials ($46.4 \pm 3.6\%$ correct, $T^+ = 15$, $N = 6$, $p > .5$; see Figure 2c).

Comparing the performance in the first three sessions with the last three sessions we found no significant improvement in any condition (incongruent: $T^+ = 17.5$, $N = 7$, $p > .5$; congruent: $T^+ = 6$, $N = 3$, $p > .1$; two-trail control: $T^+ = 6$, $N = 3$, $p > .1$).

At the individual level, all seven chimpanzees scored above chance in the congruent condition and one chimpanzee also in the incongruent condition (binomial test: $p < .05$). None of the apes scored above chance in the two-trail control condition.

These results suggest that apes were able to screen off trails that had no causal relation with the displacement of the reward with regard to the temporal order of cause and effect. Importantly, this finding cannot be explained by learning about the task-relevant contingencies over the course of this experiment. The difference between congruent and incongruent trials most likely reflects a memory deficit as in incongruent trials the chimpanzees had to remember which trail was the preexisting one. That is to say that in incongruent trials (in contrast to congruent trials) the apes could not make an informed decision based solely on the visual array at the time they had to make their choice. However, an alternative explanation might still be that the apes had a preference for the most recent trail irrespective of any causal inference. In the following experiment we examined this alternative account by presenting the apes again with two trails leading to different cups. However, this time we manipulated whether the causal trail was the preexisting trail or the most recent one.

Experiment 4

Materials and Method

Subjects. Same as in Experiment 2.

Procedure and design. There were two conditions and both involved two trails: the preexisting and recent trials (see Figure 1h and i). In both trial types, E first placed a sheet of brown paper on the platform (without a trail). In the preexisting trials, E now placed a smaller second sheet of brown paper on top of the other one that exhibited a trail toward the left or right hole. Then E placed the reward and the two red cups on the platform. The reward was in close contact to this preexisting trail. E occluded the scenery, displaced the yogurt bowl while leaving a second trail and hid it under the cup that was not at the endpoint of the preexisting trail (as in incongruent trials of Experiment 3). Then the subject could choose between the two cups.

In recent trials, E did not place the second sheet of paper with the preexisting trail on the platform before he occluded the scenery but after he had removed the screen. Instead, upon removal of the screen, the subject only saw one (causal) trail that was leading to the baited cup made by E when her view was blocked by the screen. Then E placed a small sheet of brown paper with a second trail (identical to the ones used in preexisting trials) leading to the nonbaited cup on the platform before the subject was allowed to make her choice. Therefore, in recent trials the noncausal trail was also the most recent trail. Importantly, at the time the subject was allowed to choose, there were in both conditions two symmetrical trails on the platform, each leading to one of the cups.

We administered 12 trials per session with six trials per condition. In half of the trials the reward was moved to the left and to the right, respectively. We pseudorandomized the order of trials with the restriction that no more than three consecutive trials were to same direction and no more than three consecutive trials were of the same condition. All subjects completed four sessions, for a total of 24 trials per condition.

Scoring and analysis. Same as in Experiment 1

Results and Discussion

Subjects scored significantly better in recent trials than in preexisting trials ($T^+ = 28$, $N = 7$, $p < .05$) even though the chimpanzees scored significantly above chance in both, preexisting ($69.0 \pm 5.8\%$ correct, $T^+ = 26.5$, $N = 7$, $p < .05$) and recent trials ($85.1 \pm 5.4\%$ correct, $T^+ = 28$, $N = 7$, $p < .05$; see Figure 2d).

Comparing the performance in the first two sessions with the last two sessions we found no significant improvement neither in preexisting trials ($T^+ = 15.5$, $N = 6$, $p > .1$) nor in recent trials ($T^+ = 10$, $N = 4$, $p > .1$). At the individual level, all six chimpanzees scored significantly above chance in the recent condition and three in the preexisting condition (binomial test: $p < .05$).

These results replicate the findings of Experiment 3 (incongruent condition) and, in addition, rule out that apes' performance in Experiment 3 can be attributed to a bias toward the most recent trail. In the recent condition of the current experiment, the apes in fact ignored the most recent, noncausal trail and went for the causal, preexisting trail. Importantly, learning over the course of the experiment could not account for this finding. Thus, these findings suggest that the apes were sensitive to the temporal order of cause and effect in current context.

Finally, however, it is still unclear whether the apes really followed the trails or whether they only used the trails as a cue that marked the baited cup (while taking into account the temporal order of cue-production and hiding of the reward). Therefore, we presented chimpanzees with a last experiment that involved two successive trails: the first leading from the starting point to the false, nonbaited cup, and the second trail leading from that cup to the baited cup. If the apes were following the trails, they should pick the cup at the endpoint of the two trails. If, alternatively, the apes had used the trail simply as perceptual cue that indicated the presence of the yogurt bowl they should go for the cup surrounded by most of the yogurt, that is, the nonbaited cup in the current set-up. Moreover, to probe whether two successive trails were just too complex to process for the apes at once, we manipulated, in addition, whether the apes got an update on the intermediary location of the reward after the first displacement (two-step) or not (one-step).

Experiment 5

Materials and Method

Subjects. Same as in Experiment 2.

Procedure and design. There were three trial types: infer, one-step, and two-step (see Figure 1a, j, and k). Infer trials were identical to Experiment 1 (causal condition). In one-step and two-step trials E first placed a sheet of brown paper on the platform (without a preexisting trail). Then E placed the reward and the two red cups on the platform. E occluded the scenery by means of the screen, displaced the yogurt cup while leaving a trail and hid it under one of the two cups. In the two-step condition (but not in the one-step condition), E at that point lifted the screen for 3–5 s (or longer if the subject was not looking at the platform) and the subject could visually inspect the current state of the platform. Then E occluded the platform again and displaced the yogurt bowl from that cup to the other one while leaving a second trail. Finally, E removed the screen again, pushed the platform forward and the subject was allowed to choose. Thus, the only difference between the one-step and two-step condition was that in the two-step condition subjects got an update about the location of the reward after the first displacement whereas in the one-step condition both trails were made without giving subjects such an intermediary update. The number of trials and the pseudorandomization was identical to Experiment 2.

Scoring and analysis. Same as in Experiment 1.

Results and Discussion

We found a significant effect of trial type ($F = 10.29$, $N = 7$, $df = 2$, $p < .01$). Subjects scored significantly better in infer than two-step trials ($T^+ = 28$, $N = 7$, $p < .05$). Even though the differences failed to reach the significance threshold, subjects tended to perform better in infer than one-step trials ($T^+ = 27$, $N = 7$, $p = .06$) and in one-step compared with two-step trials ($T^+ = 27$, $N = 7$, $p = .06$). The chimpanzees scored significantly above chance in infer ($92.3 \pm 4.6\%$ correct, $T^+ = 28$, $N = 7$, $p < .05$) and one-step trials ($69.0 \pm 3.3\%$ correct, $T^+ = 28$, $N = 7$, $p < .05$) but not in two-step trials ($49.4 \pm 6.1\%$ correct, $T^+ = 14.5$, $N = 7$, $p > .5$).

Comparing the performance in the first three sessions with the last three sessions we found that subjects significantly improved in

two-step trials ($T^+ = 28$, $N = 7$, $p < .05$; see Figure 3) but not in one-step ($T^+ = 17$, $N = 7$, $p > .5$) or infer trials ($T^+ = 3$, $N = 3$, $p > .5$).

At the individual level, six chimpanzees scored significantly above chance in the infer condition and two in the one-step condition (binomial test: $p < .05$). None of the apes scored significantly better than chance in the two-step condition.

The results of the one-step condition indicate that chimpanzees were not simply picking the cup that was surrounded by most yogurt (as they could have done in infer trials) but were actually following the trail to its endpoint. This finding suggests that the apes decided not merely based on a perceptual rule but considered the logico-causal relations of the task indicating that the reward was most likely hidden at the endpoint of the two successive trails.

Contrary to our expectations, the chimpanzees had more problems to solve the two-step condition. During the first sessions, the chimpanzees exhibited a strong bias toward the first hiding place. This difference between the one-step and two-step condition suggests that apes had difficulties to update the location of the hidden reward based on novel information. When they got intermediate information on the location of the reward (as in the two-step condition) the apes tended to stick to this information even though novel information indicated otherwise. Inhibitory control that was necessary to suppress the first bit of information might have acted here as limiting factor. Over the course of sessions the apes overcame this bias toward the first hiding place and, finally, their performance reached a comparable level to the one-step condition.

Interestingly, the type of error the apes made in the two-step condition within the first sessions resembles the A-not-B error in some respect as it also includes a perseveratory tendency toward previously acquired information. However, great apes have been shown not to commit the classic A-not-B error (e.g., Barth & Call, 2006; de Blois, Novak, & Bond, 1998). The crucial difference between the current task and classic A-not-B error tasks is the strength of information that subjects received about the location of the reward. In A-not-B error tasks subjects actually see where the reward has been displaced and hidden in the first place (A) and where it is subsequently transferred to (B). In the present task, the

subjects have to infer the first (A) and second location (B) of the reward based on indirect evidence supplied by the trails. Thus, “weaker” information gained by causal inference might be more susceptible for interference by prior experience. In line with that, previous research has showed that orangutans and chimpanzees succeeded to track hidden rotations and transpositions in an object displacement task when they saw the initial position of the food reward but not when the initial location was indicated by a (previously associated) landmark (Call, 2003). Call (2003) suggested that apes’ failure to update the location of the reward in the landmark condition might have been due to higher representational demands of embedded representations (the landmark represents the reward that is at a certain location) compared with simple representations (the reward is at a certain location). Similarly, the trails can also be regarded as an embedded representation (the trail indicates the presence of the reward at a certain location). According to this view, the current finding lends support to the notion that nonhuman apes have difficulties to update embedded, recursive representations.

The results of the one-step condition can also be reconciled with previous findings on invisible double displacement tasks. Collier-Baker and Suddendorf (2006) showed that when presented with two successive hidden displacements, chimpanzees searched more often in the two visited hiding locations (compared with nonvisited locations). Moreover, they found that when the chimpanzees did not find the reward in one location they searched in the other visited location. Chimpanzees’ sequential search in double invisible displacement tasks suggests that they were able to represent two successive hiding locations which might be at the basis for apes’ performance in the one-step condition of the current experiment.

General Discussion

Great apes spontaneously followed trails to locate hidden food when there was a causal (and consistent) relation between the type of reward and the trail. Moreover, chimpanzees took the temporal order of cause (reward) and effect (trail) into account—something that allowed them to differentiate between preexisting (noncausal) trails and causally relevant trails. Our data also ruled out the possibility that apes merely chose the cup that was surrounded by the largest quantity of yogurt. Taken together these findings suggest that nonhuman apes’ performance in the present task reflects causal rather than associative knowledge based on evidence for (a) the integration of temporal information about cause and effect, and (b) the impact of the logico-causal relation between reward and trail.

Nonhuman apes, like humans in the “tracks in the snow” example, used the yogurt trails (even when produced out of sight) to make inferences about their cause, that is, the displacements of the yogurt cups. Together with the evidence from inference-by-exclusion paradigms (Call, 2004, 2006b; Hill et al., 2011; Premack & Premack, 1994; Sabbatini & Visalberghi, 2008), the current task provides *prima facie* evidence for nonhuman apes’ sensitivity to unobservable constraints specific to diagnostic causal inferences. Nevertheless, apes’ causal knowledge might be limited to trails involving the food reward itself, in contrast to trails that are based on physical changes of the underlying substrate, for example, footprints in the snow or color changes of the underlying paper. In

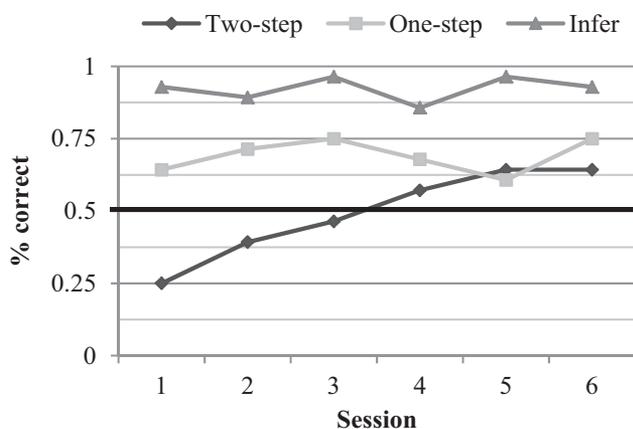


Figure 3. Experiment 5: Performance (mean per cent correct) of chimpanzees ($N = 7$) across sessions as a function of trial type (infer, one-step, and two-step).

Pilot Experiment 1 we presented 12 chimpanzees with trails left by the displacement of half a grape on a sheet of colored paper. Thus, these trails were in fact based on complex object-object relations (i.e., reward–substrate interaction). Interestingly, none of the 12 chimpanzees tested with this set-up followed the trails to their endpoint suggesting that trails based on changes of the underlying substrate are harder for them to understand. However, this notion requires further research with other type of trails (e.g., tracks in the sand) as color changes on paper caused by some fluid might go well beyond their physical knowledge, especially given that the chimpanzees had no previous experience with this type of colored paper.

In contrast to several paradigms including the reverse-reward contingency (Boysen & Berntson, 1995) and the inclined board paradigm (Call, 2007), great apes' performance in the current task was unaffected by a perceptual bias toward larger quantities of food. For instance, when confronted with two differentially inclined boards, Call (2007) found that apes preferentially selected the board with the strongest inclination (indicating a larger reward) even though they got prior information about the inferior quality of the larger reward compared with the smaller one (i.e., large carrot vs. small banana piece). In the current experiment, apes' performance was not governed by such a perceptual bias because, in the endpoint control, they avoided the cup that was surrounded by most yogurt and selected the correct cup from a logico-causal point of view. Furthermore, whereas great apes in the current paradigm were able to use temporal information about cause and effect, long-tailed macaques (*Macaca fascicularis*) failed to integrate information about the temporal order of cause and effect in the inclined board set-up (Schloegl et al., 2013).

The superior performance of apes in current paradigm compared with such previous studies might be based on minimized demands for physical knowledge. In contrast to the inclined board paradigm, for instance, the apes in the current setting did not have to take into account how one object affected the other (except for Pilot Experiment 1 in which the apes failed). Moreover, there was no need in the current paradigm to reason about hidden forces (such as gravity) and their effects as in other physical cognition studies (Cacchione & Call, 2010; Hanus & Call, 2008, 2011; Povinelli, 2011). Instead, the current task required knowledge about object permanence and hidden objects displacements—something that is well established in all great ape species (e.g., Barth & Call, 2006; Beran, Beran, & Menzel, 2005; Call, 2003; de Blois et al., 1998; de Blois et al., 1999; Natale, Antinucci, Spinozzi, & Potí, 1986).

Therefore, to investigate the extent of causal reasoning in non-human animals one might want to distinguish between physical and causal knowledge. Causal knowledge is not necessarily conditional on physical knowledge (and vice versa). More abstract causal relations independent of physical knowledge as illustrated by the “blicket detector” paradigm (Gopnik et al., 2001) and paradigms based on preconditioned arbitrary associations between events (cf. Beckers, Miller, De Houwer, & Urushihara, 2006; Blaisdell et al., 2006) might be applied in future research to shed more light on the nature of nonhuman causal reasoning.

Another interesting finding of the current experiments is that although in all trial types (except for control trials) trails were present and could be used as a discriminatory visual cue to locate the food reward, we hardly found any learning across sessions (except for the two-step condition of Experiment 5). In the causal

condition of Experiment 1, the apes immediately grasped the contingencies of the task (as indicated by the first trial analysis) and quickly reached their ceiling performance. In the arbitrary condition, they did not do so and they did not improve their performance over trials. This result confirms previous studies on causal reasoning showing that discriminative learning alone cannot explain apes' use of causal cues (Call, 2006a). It is true that the lack of attention to the demonstrations may explain a constant level of errors in all conditions. However, in the arbitrary condition, we have to assume that the apes were simply not paying attention to the relevant cue, the yogurt trail, presumably as there was no obvious relation to the expected reward. The mixed order of trial types might have also contributed to their failure to learn about the task-relevant contingencies in the arbitrary condition as we intermixed control trials in which the discriminatory cue was absent. Nevertheless, we would expect them to learn the association between the trail and the location of the pellet given a sufficient number of trials with this set-up.

In conclusion, nonhuman great apes spontaneously followed trails possessing a causal relation with the location of a hidden reward and ignored noncausal trails. Additionally, chimpanzees were able to integrate temporal information in order to diagnose the true effect of the object displacement that took place out of their sight while screening off noncausal distractors. Thus, the current findings indicate that great apes know more about the “cement of the universe” (i.e., causality, cf. Hume, 1978) than previously thought. However, whether nonhuman primates, like humans, adopt an explanatory attitude (Visalberghi & Tomasello, 1998) and intentionally use their own interventions to examine unknown causal contingencies remains a question for future research.

References

- Albiach-Serrano, A., Bugnyar, T., & Call, J. (2012). Apes (*Gorilla gorilla*, *Pan paniscus*, *P. troglodytes*, *Pongo abelii*) versus corvids (*Corvus corax*, *C. corone*) in a support task: The effect of pattern and functionality. *Journal of Comparative Psychology*, *126*, 355–367. doi:10.1037/a0028050
- Barth, J., & Call, J. (2006). Tracking the displacement of objects: A series of tasks with great apes (*Pan troglodytes*, *Pan paniscus*, *Gorilla gorilla*, and *Pongo pygmaeus*) and young children (*Homo sapiens*). *Journal of Experimental Psychology: Animal Behavior Processes*, *32*, 239–252. doi:10.1037/0097-7403.32.3.239
- Beckers, T., Miller, R. R., De Houwer, J., & Urushihara, K. (2006). Reasoning rats: Forward blocking in Pavlovian animal conditioning is sensitive to constraints of causal inference. *Journal of Experimental Psychology: General*, *135*, 92–102. doi:10.1037/0096-3445.135.1.92
- Beran, M. J., Beran, M. M., & Menzel, C. (2005). Spatial memory and monitoring of hidden items through spatial displacements by chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology*, *119*, 14–22. doi:10.1037/0735-7036.119.1.14
- Blaisdell, A. P., Sawa, K., Leising, K. J., & Waldmann, M. R. (2006). Causal reasoning in rats. *Science*, *311*, 1020–1022. doi:10.1126/science.1121872
- Blaisdell, A. P., & Waldmann, M. R. (2012). Rational rats: Causal inference and representation. In T. R. Zentall & E. A. Wasserman (Eds.), *Handbook of comparative cognition* (pp. 175–198). Oxford, UK: Oxford University Press. doi:10.1093/oxfordhb/9780195392661.013.0011
- Boesch, C., Head, J., & Robbins, M. M. (2009). Complex tool sets for honey extraction among chimpanzees in Loango National Park, Gabon.

- Journal of Human Evolution*, 56, 560–569. doi:10.1016/j.jhevol.2009.04.001
- Boysen, S. T., & Berntson, G. G. (1995). Responses to quantity: Perceptual versus cognitive mechanisms in chimpanzees (*Pan troglodytes*). *Journal of Experimental Psychology: Animal Behavior Processes*, 21, 82–86. doi:10.1037/0097-7403.21.1.82
- Burghardt, G. M. (1992). Human-bear bonding in research on black bear behavior. In H. Davis & D. Balfour (Eds.), *The inevitable bond: Examining scientist-animal interactions* (pp. 365–382). Cambridge, UK: Cambridge University Press.
- Cacchione, T., & Call, J. (2010). Intuitions about gravity and solidity in great apes: The tubes task. *Developmental Science*, 13, 320–330. doi:10.1111/j.1467-7687.2009.00881.x
- Call, J. (2003). Spatial rotations and transpositions in orangutans (*Pongo pygmaeus*) and chimpanzees (*Pan troglodytes*). *Primates*, 44, 347–357. doi:10.1007/s10329-003-0048-6
- Call, J. (2004). Inferences about the location of food in the great apes. *Journal of Comparative Psychology*, 118, 232–241. doi:10.1037/0735-7036.118.2.232
- Call, J. (2006a). Descartes' two errors: Reasoning and reflection from a comparative perspective. In S. Hurley & M. Nudds (Eds.), *Rational animals* (pp. 219–234). Oxford, UK: Oxford University Press. doi:10.1093/acprof:oso/9780198528272.003.0010
- Call, J. (2006b). Inferences by exclusion in the great apes: The effect of age and species. *Animal Cognition*, 9, 393–403. doi:10.1007/s10071-006-0037-4
- Call, J. (2007). Apes know that hidden objects can affect the orientation of other objects. *Cognition*, 105(1), 1–25. doi:10.1016/j.cognition.2006.08.004
- Cheney, D. L., & Seyfarth, R. M. (1990). *How monkeys see the world: Inside the mind of another species*. Chicago, IL: University of Chicago Press.
- Collier-Baker, E., & Suddendorf, T. (2006). Do chimpanzees (*Pan troglodytes*) and 2-year-old children (*Homo sapiens*) understand double invisible displacement? *Journal of Comparative Psychology*, 120, 89–97. doi:10.1037/0735-7036.120.2.89
- de Blois, S. T., Novak, M. A., & Bond, M. (1998). Object permanence in orangutans (*Pongo pygmaeus*) and squirrel monkeys (*Saimiri sciureus*). *Journal of Comparative Psychology*, 112, 137–152. doi:10.1037/0735-7036.112.2.137
- de Blois, S. T., Novak, M. A., & Bond, M. (1999). Can memory requirements account for species' differences in invisible displacement tasks? *Journal of Experimental Psychology: Animal Behavior Processes*, 25, 168–176. doi:10.1037/0097-7403.25.2.168
- Goodall, J., Bandora, A., Bergmann, E., Busse, C., Matama, H., Mpongo, E., . . . Riss, D. (1979). Intercommunity interactions in the chimpanzee population of the Gombe National Park. In D. A. Hamburg & E. R. McCown (Eds.), *The great apes* (Vol. 5, pp. 13–53). Menlo Park, CA: Benjamin/Cummings.
- Gopnik, A., Sobel, D. M., Schulz, L. E., & Glymour, C. (2001). Causal learning mechanisms in very young children: Two-, three-, and four-year-olds infer causal relations from patterns of variation and covariation. *Developmental Psychology*, 37, 620–629. doi:10.1037/0012-1649.37.5.620
- Hanus, D., & Call, J. (2008). Chimpanzees infer the location of a reward on the basis of the effect of its weight. *Current Biology*, 18, R370–R372. doi:10.1016/j.cub.2008.02.039
- Hanus, D., & Call, J. (2011). Chimpanzee problem-solving: Contrasting the use of causal and arbitrary cues. *Animal Cognition*, 14, 871–878. doi:10.1007/s10071-011-0421-6
- Harrison, J. F., Fewell, J. H., Stiller, T. M., & Breed, M. D. (1989). Effects of experience on use of orientation cues in the giant tropical ant. *Animal Behaviour*, 37, 869–871. doi:10.1016/0003-3472(89)90076-6
- Herrmann, E., Wobber, V., & Call, J. (2008). Great apes' (*Pan troglodytes*, *Pan paniscus*, *Gorilla gorilla*, *Pongo pygmaeus*) understanding of tool functional properties after limited experience. *Journal of Comparative Psychology*, 122, 220–230. doi:10.1037/0735-7036.122.2.220
- Hill, A., Collier-Baker, E., & Suddendorf, T. (2011). Inferential reasoning by exclusion in great apes, lesser apes, and spider monkeys. *Journal of Comparative Psychology*, 125, 91–103. doi:10.1037/a0020867
- Hume, D. (1978). *A treatise of human nature*. London, UK: John Noon.
- Kummer, H. (1995). Causal knowledge in animals. In D. Sperber, D. Premack, & A. J. Premack (Eds.), *Causal cognition: A multidisciplinary debate* (pp. 26–39). Oxford, UK: Clarendon Press.
- Natale, F., Antinucci, F., Spinozzi, G., & Potí, P. (1986). Stage 6 object concept in nonhuman primate cognition: A comparison between gorilla (*Gorilla gorilla gorilla*) and Japanese macaque (*Macaca fuscata*). *Journal of Comparative Psychology*, 100, 335–339. doi:10.1037/0735-7036.100.4.335
- Penn, D. C., & Povinelli, D. (2007). Causal cognition in human and nonhuman animals: A comparative, critical review. *Annual Review of Psychology*, 58, 97–118. doi:10.1146/annurev.psych.58.110405.085555
- Povinelli, D. (2011). *World without weight: Perspectives on an alien mind: Perspectives on an alien mind*. Oxford, UK: Oxford University Press. doi:10.1093/acprof:oso/9780198570967.001.0001
- Povinelli, D., Reaux, J., Theali, L., & Giambone, S. (2000). The support problem: Physical connection revisited. In D. J. Povinelli (Ed.), *Folk physics for apes: The chimpanzee's theory of how the world works* (pp. 254–270). New York, NY: Oxford University Press.
- Premack, D., & Premack, A. (1994). Levels of causal understanding in chimpanzees and children. *Cognition*, 50, 347–362. doi:10.1016/0010-0277(94)90035-3
- Sabbatini, G., & Visalberghi, E. (2008). Inferences about the location of food in capuchin monkeys (*Cebus apella*) in two sensory modalities. *Journal of Comparative Psychology*, 122, 156–166. doi:10.1037/0735-7036.122.2.156
- Schloegl, C., Waldmann, M. R., & Fischer, J. (2013). Understanding of and reasoning about object–object relationships in long-tailed macaques? *Animal Cognition*, 16, 493–507. doi:10.1007/s10071-012-0591-x
- Schrauf, C., & Call, J. (2011). Great apes use weight as a cue to find hidden food. *American Journal of Primatology*, 73, 323–334. doi:10.1002/ajp.20899
- Seed, A. M., & Call, J. (2009). Causal knowledge for events and objects in animals. In S. Watanabe, A. P. Blaisdell, L. Huber, & A. Young (Eds.), *Rational animals, irrational humans* (pp. 173–187). Tokyo, Japan: Keio University Press.
- Sodian, B., Taylor, C., Harris, P. L., & Perner, J. (1991). Early deception and the child's theory of mind: False trails and genuine markers. *Child Development*, 62, 468–483. doi:10.2307/1131124
- Visalberghi, E., & Tomasello, M. (1998). Primate causal understanding in the physical and psychological domains. *Behavioural Processes*, 42, 189–203. doi:10.1016/S0376-6357(97)00076-4
- Waldmann, M. R. (2000). Competition among causes but not effects in predictive and diagnostic learning. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 26, 53–76. doi:10.1037/0278-7393.26.1.53
- Waldmann, M. R. (2001). Predictive versus diagnostic causal learning: Evidence from an overshadowing paradigm. *Psychonomic Bulletin & Review*, 8, 600–608. doi:10.3758/BF03196196
- Webb, J. K., & Shine, R. (1992). To find an ant: Trail-following in Australian blindsnakes (Typhlopidae). *Animal Behaviour*, 43, 941–948. doi:10.1016/S0003-3472(06)80007-2

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