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Inferences About the Location of Food in the Great Apes (*Pan paniscus*, *Pan troglodytes*, *Gorilla gorilla*, and *Pongo pygmaeus*)

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Bonobos (*Pan paniscus*; $n = 4$), chimpanzees (*Pan troglodytes*; $n = 12$), gorillas (*Gorilla gorilla*; $n = 8$), and orangutans (*Pongo pygmaeus*; $n = 6$) were presented with 2 cups (1 baited) and given visual or auditory information about their contents. Visual information consisted of letting subjects look inside the cups. Auditory information consisted of shaking the cup so that the baited cup produced a rattling sound. Subjects correctly selected the baited cup both when they saw or heard the food. Nine individuals were above chance in both visual and auditory conditions. More important, subjects as a group selected the baited cup when only the empty cup was either shown or shaken, which means that subjects chose correctly without having seen or heard the food (i.e., inference by exclusion). Control tests showed that subjects were not more attracted to noisy cups, avoided shaken noiseless cups, or learned to use auditory information as a cue during the study. It is concluded that subjects understood that the food caused the noise, not simply that the noise was associated with the food.

One of the fundamental issues in animal problem solving is the distinction between learning and reasoning. This distinction has its roots in the debates between Köhler and Thorndike that took place in the first quarter of the last century. Whereas Thorndike (1898) argued for associative explanations based on practice and progressive improvement over trials (i.e., trial and error), Köhler (1925) maintained that mental reorganization of problem elements into a sudden solution (i.e., insight) is a fundamental component of problem solving. Nearly a century after this distinction was highlighted, it still plays an important role in current thinking about problem solving in animals and humans (Premack, 1995; Sloman, 1996). Even current debates on the mechanisms responsible for social intelligence have invariably focused around some version of these two kinds of explanations (Call, 2001; Call & Tomasello, in press; Heyes, 1994, 1998; Povinelli & Eddy, 1996).

Premack (1995) has distinguished learning from reasoning on several grounds, mostly organized around two main issues: representation and explanation. The representational issue has to do with the kind of information that individuals process. Thus, Premack (1995) indicated that learning involves associating two perceivable events, whereas reasoning involves associating a perceivable and an imagined (i.e., perceptually not available) event. The explanatory issue involves seeking causes for events. Thus, reasoning (but not learning) depends on the search causes of unexplained events and some level of understanding of the observed phenomena. In contrast, learning does not seek cognitive explanations; it just focuses on identifying regularities and associating external events.

One way to test whether individuals use reasoning or learning to solve problems consists of presenting a problem in which certain information is missing to see how subjects solve the problem. For instance, Premack and Premack (1994) presented chimpanzees with two boxes and two types of fruit (e.g., banana and apple). Chimpanzees were allowed to witness the experimenter deposit each fruit in one of the boxes so that both boxes were baited. Later, subjects saw the experimenter eating one of the fruits (e.g., banana), and the question was whether given the opportunity to select one of the boxes, they would select the box in which the experimenter had deposited the food that he was not currently eating (i.e., apple), presumably because it still contained the fruit. Chimpanzees solved this problem quickly without trial and error, showing that they were able to infer that if the experimenter was eating the banana, the box in which the banana was deposited would be empty. This is called inferential reasoning by exclusion. Note that the alternative to this inferential strategy is a discriminative learning strategy in which subjects would learn throughout multiple trials that the presence of the banana in the experimenter's mouth is a discriminative sign for choosing the other alternative. Premack (1995), however, ruled out this explanation because chimpanzees did not learn gradually to select the correct container; they selected it from the beginning.

This sort of inferential reasoning has been observed in other studies. For instance, Call and Carpenter (2001) presented chimpanzees, orangutans, and 2-year-old children with two hollow tubes and hid one piece of food inside one of them. To get the reward, subjects had to choose the baited tube. Prior to choosing, however, subjects had the opportunity to look inside the tubes to locate the reward, which many individuals did. Call and Carpenter (2001; see also Call, in press-b) observed that in the majority of trials, subjects looked inside the tubes until they saw the reward and then they made their choice. Yet in approximately 20%–30% of the trials, subjects who looked inside a tube and found it empty directly selected the other tube (without looking).

There is also one study in which a chimpanzee was able to solve inferential exclusion in the auditory modality. Hashiya and Kojima (2001) presented a chimpanzee with two pictures of people that she knew and the voice of one of them. The chimpanzee success-

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fully matched the voice with the correct picture. Then Hashiya and Kojima presented her with two pictures (one of someone she knew and the other of someone she did not know) and an unfamiliar voice. The chimpanzee correctly matched the unfamiliar voice to the unfamiliar picture.

Despite these results, there are still a number of questions that remain unanswered. Perhaps the most important question is why there are no empirical tests that directly contrast the reasoning and the learning mechanisms. Although Premack (1995) indicated that reasoning was a more likely explanation than learning because of the absence of gradual acquisition, it is still possible that subjects learned very quickly. This cannot be ruled out because Premack presented no Trial 1 performance data. Moreover, there was no test directly comparing the performance that would be expected from learning with that expected from reasoning. The lack of this comparison is particularly unfortunate because potential cases of animal reasoning are often dismissed just because learning may explain the results although no effort was made to test this possibility empirically. Second, there is not much information on auditory inferences compared with visual inferences. This is important because researchers need to know whether inferences occur in different sensory modalities and are not restricted to some of them. Finally, nothing is known about inferences in great apes other than chimpanzees. Additional information about other great apes' abilities can help to make inferences about the evolution of these abilities in hominoids.

Thus, the aim of this study was to investigate the ability of the great apes to find hidden food using different sorts of information, paying particular attention to the mechanism underlying performance. Thus, throughout the study I contrasted the reasoning–inferential explanation and the learning explanation. The general procedure was similar to Premack's (1995) and consisted of hiding food in one of two containers, giving partial information about the food and seeing whether subjects could choose the correct container. In addition, I included some tests in which I investigated whether learning alone could explain the observed results. This setup allowed me to focus on both the representational and explanatory aspects underlying Premack's analysis. I studied the representational aspect by giving visual and auditory information of various kinds. In some cases, this implied offering no visual and no auditory information about the food, and subjects had to use the absence of noise in a shaken cup (or the sight of an empty cup) to infer that the reward was located in the other cup. I studied the explanatory dimension by asking whether great apes know that the shaken food makes the noise or whether they simply associate the presence of food with the presence of the noise.

Experiment 1: Full Information

This first experiment assayed the general testing procedure and assessed whether great apes are capable of using auditory (and visual) information to find food in one of two cups.

Method

Subjects

Orangutans (*Pongo pygmaeus*; $n = 6$), chimpanzees (*Pan troglodytes*; $n = 12$), gorillas (*Gorilla gorilla*; $n = 8$), and bonobos (*Pan paniscus*; $n = 40$) housed at the Wolfgang Köhler Research Center, Leipzig Zoo (Leipzig, Germany), participated in this study. There were 18 females and 9 males ranging from 4 to 30 years of age. All bonobos and all adult chimpanzees were nursery reared, whereas all other subjects were mother reared. All subjects lived in social groups of various sizes with access to indoor and outdoor areas. Subjects were individually tested in their indoor cages and were not food or water deprived. Table 1 presents the age, sex, rearing history, and experimental participation of each subject.

Materials

Two white opaque cups (17.0 cm × 8.5 cm) with their respective tops (8.5 cm in diameter) were placed on a wooden platform about 52.0 cm apart. I used grapes and monkey chow as rewards.

Procedure and Design

The experimenter sat facing the subject behind the platform. Subjects were accustomed to this procedure and quickly approached the experimenter and sat facing him as soon as he sat behind the platform. The experimenter placed the two cups (with their tops off) on the platform behind an opaque screen. Then, the experimenter showed the reward (a grape and a piece of monkey chow) to the subject and inserted his hand in the left and right cups in succession. In half of the trials the experimenter left the reward in the left cup whereas in the other half the experimenter left the reward in the right side cup. The experimenter covered the cups with the tops, removed the screen, and moved the cups to a predetermined position on the platform and administered one of three sensory modality conditions.

Visual. The experimenter removed the top of the left cup, showed its contents to the subject by tilting the open cup toward the subject, and replaced the top on the cup. Then, the experimenter repeated the same manipulation with the right side cup. At the end of these manipulations the subjects had seen the location of the reward.

Auditory. The experimenter lifted the left cup and shook it using a sideways motion for approximately 2–3 s and replaced the cup on the platform. Next, the experimenter repeated the same manipulation with the right side cup. Shaking the baited cup produced an audible rattling noise.

No information (control). The experimenter remained motionless without either opening or shaking the cups. This condition assessed the possibility that subjects used inadvertent cues by the experimenter, the food, or the baiting procedure to find the food.

After administering each of these conditions, the experimenter pushed the platform against a acrylic plastic sheet partition with three circular holes (6.0 cm in diameter) so that the subjects could choose one of the cups located in front of one of the two extreme holes. The first container touched by the subject was scored as his or her choice.

Each subject received six 12-trial sessions (4 trials per condition per session) for a total of 24 trials per condition. All conditions were presented in random order during a session with the restriction that they were uniformly distributed across a session. That is, subjects received the same number of trials of each condition throughout a session. The position of the reward (left vs. right) was randomly determined with only the two restrictions that it appear the same number of times on each side and could not appear more than two times in succession on the same side.

Results

Figure 1 presents the percentage of correct trials across conditions for each species. A Species × Condition analysis of variance (ANOVA) on the percentage of correct trials revealed a significant effect for condition, $F(2, 52) = 126.37$, $p < .01$, and no effect for species, $F(3, 26) = 2.46$, *ns*, or Species × Condition, $F(6, 52) = 1.95$, *ns*. Post hoc analyses using the Bonferroni–Holm procedure (Holm, 1979) revealed that subjects performed better in the visual

Table 1
Age, Sex, and Rearing History and the Experiments in Which Each Subject Participated

Name	Species	Age (years)	Sex	Rearing history	Experiment participation
Robert	chimpanzee	26	M	nursery	1
Reit	chimpanzee	25	F	nursery	1, 5
Natascha	chimpanzee	21	F	nursery	1, 5
Dorien	chimpanzee	21	F	nursery	1, 5
Fraukje	chimpanzee	25	F	nursery	1, 5
Ulla	chimpanzee	24	F	nursery	1, 5
Jahaga	chimpanzee	8	F	mother	1, 2, 3, 5, 6
Fifi	chimpanzee	8	F	mother	1, 5
Sandra	chimpanzee	8	F	mother	1, 2, 3, 5, 6
Gertrudia	chimpanzee	8	F	mother	1, 5
Frodo	chimpanzee	8	M	mother	1, 5
Patrick	chimpanzee	4	M	mother	1
Gorgo	gorilla	20	M	nursery	1, 5
Bebe	gorilla	24	F	unknown	1, 5
Ndiki	gorilla	24	F	unknown	1, 2, 3, 4, 5, 6
Vimoto	gorilla	6	M	mother	1, 2, 4, 5
Viringika	gorilla	6	F	mother	1, 2, 3, 4, 5, 6
Vizuri	gorilla	6	F	mother	1, 2, 4, 5
Nkwango	gorilla	5	M	mother	1, 2, 3, 5, 6
Ruby	gorilla	4	F	mother	1, 5
Joey	bonobo	19	M	nursery	1, 5
Ulindi	bonobo	8	F	mother	1
Limbuko	bonobo	6	M	nursery	1, 2, 3, 4, 5, 6
Kuno	bonobo	5	M	nursery	1, 2, 3, 4, 5, 6
Dunja	orangutan	28	F	unknown	1, 5
Bimbo	orangutan	21	M	mother	1, 5
Pini	orangutan	13	F	mother	1, 5
Walter	orangutan	12	M	mother	1, 5
Toba	orangutan	7	F	mother	1, 5
Padana	orangutan	4	F	mother	1, 5

Note. M = male; F = female.

compared with the auditory, $t(29) = 8.67$, $p < .01$, and no information conditions, $t(29) = 24.23$, $p < .01$. Similarly, subjects performed better in the auditory compared with the no information condition, $t(29) = 6.27$, $p < .01$. Likewise, subjects performed above chance (50% correct) in only the visual, $t(29) = 55.39$, $p < .01$, and auditory conditions, $t(29) = 4.85$, $p < .01$.

Individual analyses revealed that all subjects were above chance in the visual condition and 5 gorillas, 2 bonobos, and 2 chimpanzees were above chance in the auditory condition (Binomial test: $p < .01$). In contrast, none of the orangutans were above chance in the auditory condition. In fact, using this measure, I found orangutans were statistically less successful as a group than were gorillas (0% vs. 63%; Fisher test: $p = .03$) but were comparable with bonobos (0% vs. 50%; Fisher test: $p = .03$) or chimpanzees (0% vs. 17%; Fisher test: *ns*). Five of the 8 great apes who were above chance in the auditory condition made no mistakes. In contrast, none of the subjects were above chance in the no information condition (Binomial test: *ns*). To analyze any potential learning effects, I compared the subjects' performance across 6-trial blocks in the visual and auditory conditions. There was no change in performance across blocks of trials for the visual, $F(3, 87) = 0.2$, *ns*, or auditory conditions, $F(3, 87) = 0.5$, *ns*.

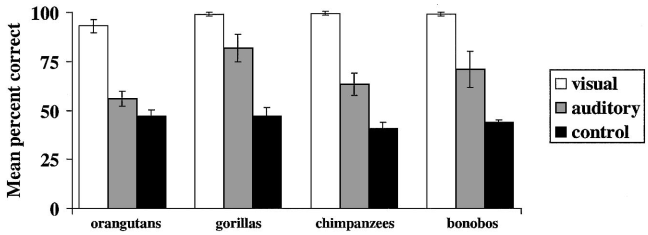

Figure 1. Mean percentages (with standard error bars) of correct trials across conditions for each species in Experiment 1.

Discussion

Subjects succeeded in using auditory (and visual) information to find the food, but they failed to do so in the absence of such information. Therefore, these results cannot be attributed to extraneous cues such as food smell, the baiting procedure, or experimenter-given cues. Moreover, individuals used auditory (and visual) information spontaneously because it occurred without training and without any evidence of learning during the test. There was some indication, albeit weak, that orangutans performed worse than gorillas in the auditory condition. The explanation for this result remains unclear and future studies should be aimed at investigating this possible divergence between great ape species further.

Although this experiment established that great apes were able to use auditory (and visual) information to locate food, it is unclear whether these results represent a case of inferential reasoning. It can also be explained by associating the presence of an auditory cue with the presence of food that would have occurred before the test started. Another possibility is that subjects may have been attracted to a cup that makes noise, simply because it calls their attention more. To test these possibilities and to see whether inferences were involved in solving this problem, I conducted the next experiment in which the auditory cue was eliminated in some conditions.

Experiment 2: Partial Information

In this experiment, I investigated whether subjects were able to find the food using partial information. In some cases I offered information about both containers whereas in other cases I offered information about either the baited or the empty container. This last condition was particularly important because subjects did not have perceptual access to the food either by seeing it or hearing it.

Method

Subjects

All subjects who were above chance in the auditory condition of the previous experiment participated in this study (see Table 1). These were 5 gorillas, 2 chimpanzees, and 2 bonobos.

Materials

The materials in Experiment 2 were the same as in Experiment 1.

Procedure and Design

The general procedure was identical to that of Experiment 1. The experimenter baited one of the cups and offered some information about the contents of the cups, and subjects made a choice (indicated by touching one of the cups). As in Experiment 1, the experimenter offered visual, auditory, or no information (control condition) regarding the food location. However, in the current experiment the experimenter also manipulated the amount of information provided to the subject. There were three possibilities.

Both. The experimenter showed the contents of both cups (visual both condition) or shook both cups (auditory both condition). These conditions were identical to the vision and auditory conditions of Experiment 1.

Baited. The experimenter showed the contents of the baited cup (visual baited condition) or shook the baited cup (auditory baited condition) and lifted (without opening or shaking) the empty cup.

Empty. The experimenter showed the contents of the empty cup (visual empty condition) or shook the empty cup (auditory empty condition) and lifted (without opening or shaking) the baited cup.

In addition to these six conditions (2 sensory modalities × 3 information types) the experimenter administered a control condition in which no information regarding the location of food was provided. In this condition, the experimenter lifted both cups in succession without opening or shaking them.

Each subject received twelve 12-trial sessions for a total of 16 trials for each of the six experimental conditions and 48 trials for the control condition. The randomization procedures and restrictions for administering the various conditions and reward position were identical to those of Experiment 1.

Results

Figure 2 presents the percentage of correct trials across conditions. I did not make any interspecific comparisons because of the small sample size. A repeated measures ANOVA with the factor sensory modality (visual and auditory) and amount of information (both, baited, and empty) on the percentage of correct trials revealed a significant effect for modality, $F(1, 8) = 25.99$, $p = .01$; amount of information, $F(2, 16) = 10.04$, $p = .01$; and Modality × Amount of Information, $F(2, 16) = 11.32$, $p = .01$.

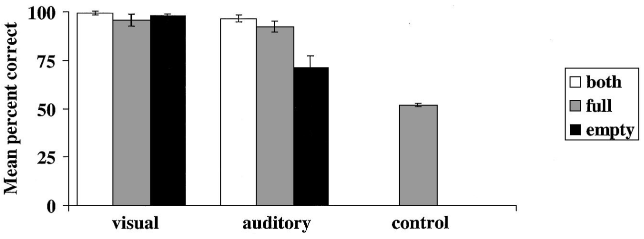

Figure 2. Mean percentages (with standard error bars) of correct trials across conditions in Experiment 2.

A comparison within each modality indicated that there were no significant differences across the various amounts of information in the visual condition, $F(2, 16) = 1.90$, *ns*. Conversely, there were significant differences across conditions in the auditory modality, $F(2, 16) = 11.54$, $p = .01$. Post hoc analyses using the Bonferroni–Holm procedure revealed that there were no significant differences between the both and baited conditions, $t(8) = 1.63$, *ns*. In contrast, subjects performed worse in the empty condition compared with the both condition, $t(8) = 4.38$, $p < .01$, and baited condition, $t(8) = 2.83$, $p = .02$. Nevertheless, subjects performed better in the auditory empty condition (or any other condition) than in the control condition, $t(8) = 3.21$, $p = .01$. Likewise, subjects performed above chance (50% correct) in all information conditions, $t(8) > 3.76$, $p < .01$, in all cases.

Individual analyses revealed that 2 gorillas (Ndiki and Vizuri) and 1 bonobo (Limbuko) were above chance in the auditory empty condition (Binomial test: $p < .05$), whereas all subjects were above chance in all the remaining conditions, except the control condition in which no subject was above chance.

To analyze any potential learning effects, I compared the subjects' performances across 6-trial blocks across modalities and amount of information. There was no change in performance across blocks of trials, $F(3, 24) = 1.6$, *ns*, and no Block × Amount of Information effect, $F(6, 48) = 0.50$, *ns*, for the visual or auditory conditions.

Discussion

Subjects were capable of selecting the correct container even without seeing or hearing the food inside it and without any evidence that learning took place during the test. This performance contrasted with the control condition, in which they failed to select the correct container. The results on the visual modality corroborate previous findings regarding inferences about hidden food (Call, in press-b; Call & Carpenter, 2001; Premack & Premack, 1994). Subjects performed equally well (and at very high levels) regardless of whether they could see the food inside the container. These results contrast with the difficulty of acquiring exclusion with arbitrary visual matching to sample (Tomonaga, Matsuzawa, Fujita, & Yamamoto, 1991; Yamamoto & Asano, 1991; but see Tomonaga, 1993), although note that those studies used more complex discrimination procedures than did the present one.

Results on inferences about seen food can be extended to the auditory modality. Subjects were capable of selecting the baited container above chance even when they had not heard any noise from it. It is true that there was a decrement in performance compared with those auditory conditions in which subjects heard the sound of the food, but it is important to note that this was still significantly better than the control condition. This result agrees with data on exclusion performance in auditory modality in 1 chimpanzee (Hashiya & Kojima, 2001) and supports the idea that subjects may be using inferential reasoning to solve this problem, not just simply using the presence of the sound as a discriminative cue to find the food or being attracted to the baited cup because the noise it produced. Still, one could argue that subjects were not making any inference, they were simply avoiding the noiseless shaken cup. Recall that in the previous experiment, the noiseless (empty) shaken cup was never rewarded because it was always paired with the noisy (baited) shaken cup. Therefore, the noiseless shaken cup may have become an aversive stimulus that subjects learned to avoid. I tested this possibility in the next experiment.

Experiment 3: Avoiding the Noiseless Shaken Cup

In this experiment, I investigated the possibility that subjects were avoiding the shaken silent cup in the previous experiment, so the shaken silent cup was presented together with a rotated silent cup. Both cup presentations shared the same features of movement and lack of noise. If an avoidance of the noiseless shaken cup could explain the results of the previous experiment, subjects should prefer the noiseless rotated cup compared with the noiseless shaken cup in the current experiment.

Method

Subjects

All subjects who participated in Experiment 2 participated in Experiment 3, except Vimoto and Vizuri (who were not available at the time of testing; see Table 1).

Materials

The materials in Experiment 3 were the same as in Experiment 1.

Procedure and Design

The general procedure was identical to that of Experiment 1. The experimenter baited one of the cups (or pretended to bait; see below) and offered some information about the contents of the cups, and subjects made a choice (indicated by touching one of the cups). Here I presented the following conditions.

Shake–shake. This was the same as the auditory both condition in Experiment 2.

Shake–rotate. The experimenter followed the same baiting procedure as in the previous condition but left both cups empty without the subject's knowledge. Then the experimenter shook one cup (as in the previous condition) and turned the other one upside down (and upside up again).

Control. This was the same as the no information condition in Experiment 2.

Each subject received one 24-trial session (8 trials per condition). One subject required two sessions to complete the 24 trials. The randomization procedures and restrictions for administering the various conditions and reward position were identical to those of previous experiments.

Results

Figure 3 presents the percentage of correct trials across conditions. Subjects did not avoid the empty shaken cup. On the contrary, they significantly preferred it to the empty rotated cup, $t(6) = 2.52$, $p < .05$. As in previous experiments, subjects were significantly above chance in the shake–shake condition (100% trials correct) but not in the control condition $t(6) = 0.0$, *ns*.

Discussion

The hypothesis that avoidance of the noiseless shaken cup could explain the results of Experiment 2 was not supported. When presented with a noiseless shaken cup and a rotated silent cup, subjects indeed preferred the shaken silent cup. Thus, the results of Experiment 2 cannot be attributed to avoidance of the noiseless shaken cup, but they may represent genuine inferences regarding the location of food. Indeed, the preference for the shaken silent cup found in the current experiment make the results of Experiment 2 even more remarkable, because it appears that subjects had a preference for the shaken empty cup. And still, in that experiment they overcame this preference to select the cup that was not shaken but contained the food.

One could argue that subjects may have avoided the rotated movement in the current experiment because of its novelty. However, this explanation would fail to account for the choices subjects made in Experiment 2, in which they selected a novel action such as raising the cup in the air over the familiar shake of the empty cup.

Thus, the idea that subjects know that sound is linked to certain movements and that those movements are produced by the food gains further credibility. To test this idea further, in the next experiment I investigated whether subjects could discriminate between movements that are likely to produce noise and movements that are not.

Experiment 4: Shaken Not Stirred

In this experiment, I presented a noiseless shaken cup with a noiseless cup that was stirred in a circular motion. Both cup presentations shared the same features of movement and lack of

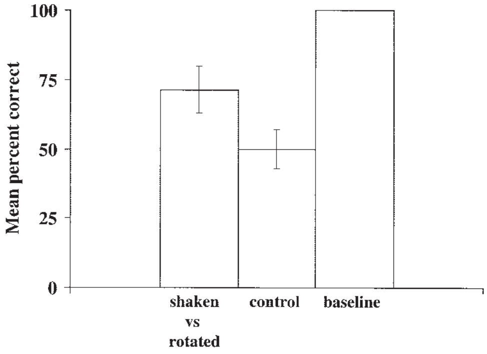

Figure 3. Mean percentages (with standard error bars) of correct trials in the shake–shake and control conditions in Experiment 3. The value in the shake–rotate condition represents the mean percentage of trials in which subjects selected the shaken over the rotated cup.

noise, with the difference that one of them should make noise if the food were inside (i.e., the shaken cup) whereas the other should not (i.e., the stirred cup). The question was whether subjects would choose the stirred cup in this situation.

Method

Subjects

Two gorillas and 1 bonobo who were above chance in the auditory empty condition of the previous experiment participated in the current experiment. In addition, to compare their performance with the other great apes (see Table 1), I tested 3 other great apes (2 gorillas and 1 bonobo) who had been included in the previous study but who were not above chance in the auditory empty condition.

Materials

The materials in Experiment 4 were the same as in Experiment 1.

Procedure and Design

The general procedure was identical to that of previous experiments. The experimenter baited one of the cups and offered some information about the contents of the cups, and subjects made a choice. Here I presented the following conditions.

Shake baited–stir empty. The experimenter shook the baited cup (producing an auditory cue) with an up-and-down motion (note that this is a different shaking motion to that of previous experiments) and stirred the empty cup. Stirring consisted of holding the cup from the top part and giving it a gentle rotational movement with the wrist similar to the one used to stir liquid in a glass with a spoon.

Shake empty–stir baited. This was the same as the previous condition except that the experimenter shook the empty cup and stirred the baited one so that there was no audible sound coming from the cups.

Control. The experimenter stirred both cups.

Each subject received four 12-trial sessions except Ndiki, who received two 24-trial sessions. Ndiki also received 10 additional control trials to clarify her results in the initial control trials. The randomization procedures and restrictions for administering the various conditions and reward position were identical to those of previous experiments.

Results

Table 2 presents the percentage of correct trials across conditions for each subject. All subjects were above chance in the shake baited–stir empty condition (Binomial test: $p < .05$) and none in the control condition (Binomial test: $p < .05$, in all cases). More important, all 3 great apes who were above chance in the auditory empty condition in the previous experiment also were above chance in the shake empty–stir baited condition in the current experiment (Binomial test: $p < .05$). In contrast, none of the great apes who failed the auditory empty test in the previous study were above chance in the empty test in the current experiment (Binomial test: *ns*). Individual comparisons between the empty and control conditions confirmed these results. All passers scored significantly higher in the empty condition than in the control condition (Fisher test: *ns*, in all three cases), whereas none of the subjects who failed did so (Fisher test: *ns*, in all three cases). Thus, subjects interpreted no auditory cue in the novel shaken condition as an empty cup but not when the cup was stirred.

Table 2
Percentage of Correct Trials in Each of the Three Conditions of Experiment 4

Name	Trial result	Condition Shake empty–stir baited	 Shake baited–stir empty	 Control
Vizuri	pass	94.4*	94.4*	58.3
Ndiki	pass	77.8*	94.4*	50.0[a]
Limbuko	pass	94.4*	94.4*	63.6[a]
Vimoto	fail	38.9	100.0*	50.0
Viringika	fail	50.0	83.3*	41.7
Kuno	fail	72.2	100.0*	58.3

[a] Based on 22 trials.
* $p < .05$.

There was no change in performance across 12-trial blocks for any of the successful subjects in the shake empty–stir baited condition (Fisher tests: *ns*, in all three cases).

Discussion

Subjects successfully selected the noiseless stirred cup over the noiseless shaken cup. It is not possible to explain these results invoking an avoidance of the shaken cup for three reasons. First, subjects did not avoid a noiseless shaken cup in Experiment 3, they actually preferred it. Second, the shaking motion in this experiment, like the stirring motion, was novel, that is, they were presented in this experiment for the first time. Third, subjects who had not passed the previous test but were included in the current experiment for comparative purposes behaved very differently. They did not distinguish between shaking and stirring, suggesting that these motions per se did not lead subjects to prefer them.

Thus, it seems that subjects' inferences are not tied to specific motions or the presence or absence of certain cues. Subjects combine the container's movements with the noise it produces (or does not produce). In other words, a noiseless stirred container is not treated the same way as a noiseless shaken container. This suggests that subjects attribute to certain actions the power to create some results—some great apes know that certain movements (i.e., vertical shaking), but not others (i.e., circular stirring), produce noise.

A history of learning is often invoked to explain results such as those presented here. Subjects may have merely learned to associate the presence of noise with food, avoid silent cups, or simply to be more attracted to stimuli with an auditory component. All these explanations have in common that subjects have little insight into the underlying physical and logical principles underlying this task, in particular, the causal–logical relation between the cup movement, the food, and the auditory cue. If subjects have none of those insights (and therefore play no role in their problem solving skills), it is expected that provided with comparable contingencies with those presented in previous experiments subjects will be able to solve the problem. In the next two experiments I investigated whether subjects do indeed take advantage of those contingencies and cues after the causal–logical structure is removed.

Experiment 5: Learning to Use an Auditory Cue

In this experiment, I presented an auditory cue consisting of noisily tapping on the baited cup to indicate the presence of food and silently tapping on the empty cup to indicate the presence of food. So the movements directed to both cups were identical, with the only difference being that an auditory cue signaled the presence of food. This is analogous to Experiment 1, in which the shaking movements applied to the cups were identical but produced different auditory cues due to the movement of the food inside. I chose the tapping procedure because, like in the shake conditions, the auditory cue resulted from something hitting against the cup, and therefore both auditory cues (the one in the current experiment and that in previous experiments) had some perceptual similarity If subjects had simply learned to associate an auditory cue with the baited container, they should pass this test without difficulty.

Method

Subjects

All subjects who participated in Experiment 1 participated in Experiment 5, except Robert, Patrick, and Ulindi (who were not available at the time of testing; see Table 1).

Materials

The materials in Experiment 5 were the same as in Experiment 1.

Procedure and Design

The general procedure was identical to that of previous experiments. The experimenter baited one of the cups and offered some information about the contents of the cups, and subjects made a choice. Here I presented the following two conditions.

Tapping. The experimenter tapped onto the top of the baited cup with the finger (3–5 times) with or without making a sound depending on whether the cup was baited or empty, respectively. The experimenter used the same hand motions toward both cups except that The experimenter produced a noise only when tapping on the baited cup. Prior informal testing had shown that subjects were capable of hearing the tapping sound because they oriented toward it (e.g., turned around and looked at the cup) if they were not looking when the experimenter tapped on the cup.

Control. The experimenter lifted both cups (same as the control condition in Experiment 2).

Each subject received four 12-trial sessions, except Sandra, who received two 12-trial sessions and one 24-trial session. The randomization procedures and restrictions for administering the various conditions and reward location were identical to those of previous experiments.

Results

There were no significant differences between the tapping (50.8% correct) and the control condition (48.3% correct), $t(26) = 0.81$, *ns*. Moreover, the tapping condition was not significantly above chance, $t(26) = 0.28$, *ns*. Individual analyses revealed that only 1 (4%) chimpanzee (Sandra) was above chance in the tapping condition (Binomial test: $p < .01$) and none in the control condition.

Individuals who succeeded in the auditory condition of Experiment 1 were not significantly better in the tapping condition than those who had failed (56.9% vs. 47.7%), $t(25) = 1.65$, *ns*. Comparing the subjects' performance across 6-trial blocks for the cue condition produced no evidence that subjects had started to learn to use the cue after 24 trials, $F(3, 78) = 0.08$, *ns*.

Discussion

Subjects were unable to use or learn to use the auditory cue as an indicator for the presence of food. This result is particularly striking because this test was conducted after Experiments 1 and 2 were completed. Recall that in both those experiments subjects were capable of using the auditory cue produced by shaking the baited cup—with some subjects demonstrating an errorless performance. Thus, even though subjects were already using an auditory cue successfully in previous experiments, they were unable to transfer it into this test.

Subjects' poor performance in this test also undermines the general learning to associate an auditory cue with food explanation. For one thing, it is difficult to understand why subjects would be able to use the auditory cue in Experiment 1 but not the auditory cue in the current experiment. Recall that both cues share some common auditory features because both resulted from hitting the cup (with food or with the finger). Moreover, if auditory specificity is so important (i.e., the cue they learned in the past should resemble the tested cue), then it hard to see why then they did so well in the initial test, because it is very unlikely that cue used in Experiment 1 was identical to the one that they had presumably learned in past. Note that the great apes had never encountered the cups that I used prior to the test.

Despite these arguments, someone could still argue that the auditory features of each cue were different enough to make the results of this test inconclusive. To remedy this situation, I ran a last control test in which I recorded the sound of the food as it is shaken and presented it to the subjects as the auditory cue instead of the tapping with noise.

Experiment 6: Audiotape-Recorder Test

In this experiment, I presented an auditory cue consisting of playing back the recorded sound made by shaking a baited cup to indicate the presence of food. I paired this condition with a condition in which no sound was produced but maintaining the movements directed to this cup identical to those performed on the baited cup during the playback. The idea is the same as that of the previous experiment but with an auditory cue that was more similar to what subjects experience when the experimenter shook a baited cup.

Method

Subjects

All subjects who participated in Experiment 2 participated in Experiment 6, except Vimoto and Vizuri (who were not available at the time of testing; see Table 1). These were 3 gorillas, 2 chimpanzees, and 2 bonobos.

Materials

The materials in Experiment 6 were the same as in Experiment 1, plus an audiotape recording of the sound made by the baited shaken cup for presentation in the audiotape-recorded trials.

Procedure and Design

The general procedure was identical to that of previous experiments. The experimenter baited one of the cups and offered some information about the contents of the cups, and subjects made a choice (indicated by touching one of the cups). Here I presented the following three conditions.

Recorded sound. The experimenter held an audiotape recorder on top of the baited cup and played back the recorded sound of a baited shaken cup or no sound depending on whether the cup was baited or empty, respectively. The experimenter used the same motions toward both cups except that the experimenter played back the recorded sound only on top of the baited cup.

Auditory baited. This was the same as the auditory baited condition in Experiment 2.

Control. This was the same as the no information condition in Experiment 2.

Each subject received one 24-trial session (8 trials per condition). The randomization procedures and restrictions for administering the various conditions and reward location were identical to those of previous experiments.

Results

Figure 4 presents the percentage of correct trials across conditions. A repeated measures ANOVA on the percentage of correct trials revealed a significant effect of condition, $F(2, 12) = 18.44$, $p < .01$. Post hoc analyses using the Bonferroni–Holm procedure revealed that subjects performed better in the auditory baited compared with the recorded sound, $t(6) = 4.60$, $p < .01$ and control conditions, $t(6) = 6.18$, $p = .01$. In contrast, there were no significant differences between the recorded sound and the control conditions, $t(6) = 0.2$, *ns*. Likewise, subjects performed above chance (50% correct) in the auditory baited, $t(6) = 27.0$, $p < .01$, but not in the recorded, $t(6) = 1.70$, *ns*, or control conditions, $t(6) = 0.83$, *ns*. Only 1 out of 7 subjects was above chance in the recorded sound condition (Binomial test: $p < .05$).

Discussion

Subjects were unable to use the recorded auditory cue to find the food. Thus, the acoustic similarity of the cue did not seem to explain the failure to use or learn to use the cue in the previous experiment.

General Discussion

Great apes were able to find the hidden food using either partial visual or auditory information. This involved in some cases selecting a noiseless lifted cup over a noiseless shaken cup. Furthermore, a minority of subjects also selected a noiseless stirred cup over a noiseless shaken cup, even though they did not avoid the noiseless shaken cup in a control test.

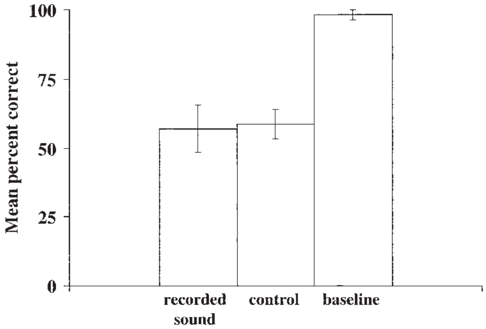

Figure 4. Mean percentages (with standard error bars) of correct trials across conditions in Experiment 6.

The current results cannot be reduced to simple explanations such as using an auditory cue to direct their attention to a certain location because subjects also succeeded in those conditions in which there were no auditory cues. Similarly, the use of inadvertent cues such as given by the experimenter (i.e., Clever Hans effect), the food, or the baiting procedure cannot account for these results because subjects systematically failed to find the food when no information was given in control tests.

Another possibility is that subjects learned to respond correctly without any insight into the structure of the problem. However, there are several reasons that make this possibility unlikely. First, there was no evidence that during the test subjects either learned to avoid certain configurations (e.g., noiseless shaken cup) or learned to respond to particular configurations (e.g., noisy cup). Even very fast learning cannot account for these results because some subjects never made a single mistake and most subjects selected correctly from Trial 1.

Second, invoking a previous history of reinforcement as the sole explanation for these results is also problematic. If subjects had learned to associate a noise with food in the past, it is unclear why they failed the test in which they could use a noise to locate the food (Experiment 5), especially given the fact that they were tested after they had solved the initial problem. One could argue that the tapping noise was too different from what they experienced in the past. However, this argument is problematic because if the cue had to be so specific to work, it is unclear why they solved the initial test (Experiment 1) given that it was the first time they heard that noise. Also recall that using an audiotape recording of the auditory cue did not alter the results.

Thus, it is unlikely that these results are solely based on learning to associate a cue with a response without any insight into the structure of the problem. Instead, it is conceivable that subjects used inferential reasoning to solve this problem. There are two additional pieces of evidence regarding the representation of stimuli and the explanation of the causal structure of the problem that support this conclusion. I focus on these two aspects, in turn.

Representation

Most previous studies have focused on making inferences on the visual modality. Two studies have shown that chimpanzees and orangutans can choose the baited container on the basis of seeing the experimenter consume the contents of one of the two containers or simply seeing one of the containers empty (Call & Carpenter, 2001; Premack & Premack, 1994). Because subjects solved this problem suddenly, not gradually, it is conceivable that insight rather than trial-and-error learning was implicated. The current study has also found very robust evidence of inference by exclusion in the visual modality in the 4 great apes, not just the chimpanzees. In addition, this study provided clear evidence of inferential processes in the auditory modality. These results are even more impressive than those in the visual modality because subjects did not even see any empty container (so that they could simply avoid them) or certain stimuli that had been placed in one of the containers. Here, subjects had to choose on the basis of a combination of the presence or absence of the auditory cue and the type of movement of the cup. At the representational level this seems a much more demanding task than those based on the visual modality.

Explanation

One of the most important differences between learning and reasoning is that in the latter subjects seek causes for events, not just associate certain stimuli. The current study provides two lines of evidence that support the idea that subjects sought causal explanations at some level.

First, there was a marked contrast between those experiments in which the cue and the food held a nonarbitrary relation (a logical necessity according to Piaget, 1952) as opposed to an arbitrary relation. Thus, subjects effectively used the auditory cue produced by shaking the cup (a nonarbitrary relation) to find the food, but they failed to use the auditory cue produced by tapping the cup (an arbitrary relation). In other words, subjects did well when there was a nonarbitrary (logical necessity) connection between the noise and the food but not when the relation was arbitrary (i.e., the cue could have been used to indicate the empty cup). Note that both cues had the same predictive power because they always reliably indicated the presence of food. Moreover, they also produced comparable auditory stimulation, particularly in the case of the audiotape recording of the actual auditory stimulus produced by shaking the cup.

This stark contrast between arbitrary and nonarbitrary connections corroborates previous findings. Whereas those studies that investigated nonarbitrary relations found positive and robust results (Call & Carpenter, 2001; Hashiya & Kojima, 2001; Premack & Premack, 1994), those studies that used arbitrary relations found that acquiring exclusion with arbitrary visual stimuli is difficult (Tomonaga et al., 1991; Yamamoto & Asano, 1991). Tomonaga (1993) argued that the history of reinforcement explained the difficulty in acquiring exclusion in arbitrary visual matching to sample. Similarly, Hashiya and Kojima (2001) attributed their positive results to the nondifferential history of reinforcement across stimuli. I do not think the history of reinforcement is the key, but the nature of the relation between the stimuli: arbitrary versus nonarbitrary.

One could argue that the difference between arbitrary and nonarbitrary relations is due to the nature of the arbitrary cues that were used. However, this is not the case, because the performance on visual discrimination of color, shape, or presence of certain stimuli (all arbitrary relations) is comparable with the results reported here for arbitrary relations (Experiments 5 and 6) and much worse than those involving nonarbitrary relations (Call, in press-a; Call & Tomasello, 1998, Experiment 1). Social cues fare no better, requiring, in many cases, numerous trials that do not always end up in successful performance (Call, Agnetta, & Tomasello, 2000; Call, Hare, & Tomasello, 1998; Tomasello, Call, & Gluckman, 1997). For instance, using arbitrary auditory cues produced worse results than those in current study with nonarbitrary cues, at least for chimpanzees (Call et al., 2000).

The second line of evidence supporting the idea that subjects seek explanations is that some subjects showed some specific knowledge about the kinds of movement on a cup that are likely to create noise (Experiment 4). Admittedly, the weight of the evidence on this issue is currently less than that provided by the distinction between arbitrary and nonarbitrary relations, but further research may produce additional data supporting this point. Particularly important will be those studies presenting novel cup movements and blocking the reward's free movement, for instance, by stuffing a cloth inside the cup in full view of the subject.

Although learning without insight into the problem structure (the reasons behind certain phenomena) seems an unlikely explanation for the current results, this is not to say that experience plays no role in solving these problems. It probably does. However, experience is not necessarily the same as learning fixed rules and stimuli relations; there is also an important component on abstracting knowledge from those experiences that can be used to solve problems. Although this is my working hypothesis (Call, 2001; Tomasello & Call, 1997), it is conceivable that some of this knowledge that I have uncovered may be part of a core knowledge system (Baillargeon, 1995; Spelke, Phillips, & Woodward, 1995). Future studies should test this possibility, particularly focusing on the interaction between such core knowledge system and the role of experience (Baillargeon, 1995).

In conclusion, I found evidence of inferential reasoning in the visual and auditory modality. Admittedly, only a minority of subjects, ranging between 30% and 10% of the subjects tested, fully mastered the most complex problems. However, note that those subjects consistently performed well in the experimental conditions while failing the corresponding control conditions. Thus, this study illustrated the ability and the limits of individual subjects in making inferences about hidden food. Overall, these results suggest that great apes do not simply associate an auditory cue with food, but they know something about the causal connection between the cue and the presence of food and, for a minority of subjects, about the movements that are likely to produce certain auditory cues. In other words, subjects know more than that the noise appears in the same location as the food, but instead it is argued that they know that the food causes the noise.

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