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Apes know that hidden objects can affect the orientation of other objects ☆

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Abstract

Four bonobos, seven gorillas, and six orangutans were presented with two small rectangular boards on a platform. One of the boards had a piece of food under it so that it acquired an inclined orientation whereas the other remained flat on the platform. Subjects preferentially selected the inclined board. In another experiment, subjects were initially presented with two inclined boards and a transformation took place in which one of the boards fell flat to the platform while the other remained inclined. Subjects also preferred the board that remained inclined. Two additional experiments highlighted some of the possible limitations of their reasoning in this task. Presented with two inclined boards, one of which was visibly supported by a piece of wood, they failed to systematically select the unsupported one whose only reason for being inclined was the presence of the reward. Another experiment presented two rewards in each trial (instead of the customary one) in one of the following two combinations: large banana vs. small carrot or small banana vs. large carrot. Prior to the test, E presented both rewards to the subject and then hid each of them under one of the boards so that both boards were differentially inclined due to the different sizes of the rewards involved. Although subjects selected the board that showed a greater inclination (thus securing the larger reward), they disregarded the type of food that was involved. This often meant that they chose the large carrot over the small banana even though they reversed such a choice when the rewards were not occluded by the boards. Providing subjects with a 'reminder' of the type of reward hidden under the boards did not alter the original results. There was no evidence of learning throughout the various experiments and control tests ruled out the possibility of inadvertent cuing by

the experimenter, poor performance due to a lack of motivation, or good performance due to a predisposition to select objects with sloped surfaces. It is concluded that subjects made some inferences about the reason for the inclined orientation of the boards, and not simply associated an inclined orientation with the presence of the reward.

1. Introduction

Traditionally, Piagetian tasks of object permanence have been taken as one of the hallmarks of representational skill in children. According to this view, at around 18 months of age infants become capable of representing invisible object displacements and have fully developed the notion that objects continue to exist even when they are not perceived (Piaget, 1954). This dominant view, however, has been challenged in recent years. For instance, Baillargeon, Spelke, and Wasserman (1985) conducted a ground-breaking experiment on the arrested motion phenomenon (Baillargeon, 1995) in which 5-month-old infants took into account the presence of an object that was not visually available in anticipating the movement described by a barrier. In the initial phase of the experiment, infants were habituated to the sight of a barrier describing a 180° back-and-forth flapping motion on a table. Then, an object was placed just behind the barrier so that when the moving barrier reached the object, it should stop. Subjects were shown two events. In one event the barrier stopped at the point where it met the object. In the other event, the barrier completed its usual 180° movement to which subjects had been habituated, thus virtually going through the object. Infants showed surprise at this latter outcome and not the outcome in which the barrier stopped once it reached the position occupied by the object, even though this motion pattern was novel for them. The authors interpreted this result as evidence that subjects knew that the object behind the barrier continued to exist despite its perceptual unavailability, thus challenging the notion of non-permanence in young infants.

This initial study triggered the development of the productive field of infant reasoning about phenomena such as gravity, solidity, continuity, or collision (see Baillargeon, 1995; Spelke, Phillips, & Woodward, 1995, for reviews). Compared to the other phenomena, arrested motion (or the closely related unveiling phenomenon, Baillargeon, 1995) has received comparatively little research attention. Baillargeon and DeVos (1994, cited in Baillargeon, 1995) presented 9-month-old infants with two cloths lying side by side on a table. One cloth lay flat on the table while the other exhibited a marked protuberance due to the presence of a toy under it. Upon occluding each cloth with a screen perpendicular to the table the experimenter either removed the toy from the protruding cloth (possible event) or the flat cloth (impossible event). Infants looked longer at the impossible event compared to the possible event. Baillargeon (1995) interpreted this result as evidence that infants inferred that an object was hidden under the protruding cloth. In another study, Baillargeon and DeVos (1994, cited in Baillargeon, 1995) found that 13-month-old infants were also

sensitive to the size of the protuberance. Upon witnessing two cloths on a table each exhibiting protuberances of different sizes, they looked longer when the experimenter extracted a large toy from the cloth with the small protuberance (impossible event) than when the large toy was extracted from the cloth with the large protuberance (possible event). This means that infants at this age took into account the size of objects hidden under the cloths so that larger objects were expected behind cloths with larger protuberances. Using the arrested motion paradigm described previously, Baillargeon (1991) found that even 6-month-old infants were sensitive to the magnitude of the event violation. Thus, infants at this age already have robust knowledge about the effect that the presence of a solid object may have on the orientation or position of another object that is resting on top of it.

The notion of object concept has received considerable attention from a comparative perspective (see Doré & Dumas, 1987; Tomasello & Call, 1997 for reviews). There is considerable evidence indicating that many species expect objects to continue to exist after undergoing some sort of occlusion event and can retrieve objects that have disappeared from sight (e.g., Doré, Fiset, Goulet, Dumas, & Gagnon, 1996; Hauser, 2001; Regolin, Vallortigara, & Zanforlin, 1995; Santos & Hauser, 2002; Tinklepaugh, 1928; Vallortigara, Regolin, Rigoni, & Zanforlin, 1998). Cats, dogs, squirrel monkeys and some birds can cope with visible displacements of objects (Collier-Baker, Davis, & Suddendorf, 2004; de Blois, Novak, & Bond, 1998; Doré et al., 1996) while parrots and apes can even cope with various double invisible displacements (Call, 2001; de Blois et al., 1998; Pepperberg, Willner, & Gravitz, 1997). Although there are hints that some monkey species may be able to solve double invisible displacements (e.g., Mendes & Huber, 2004; Schino, Spinozzi, & Berlinguer, 1990), this evidence is weaker than that found in apes and parrots.

Compared with the success of some paradigms such as the classical object permanence series (Piaget, 1954), other paradigms such as the arrested motion have not significantly contributed to the comparative literature on the object concept. Yet, the use of this paradigm is important for at least two main reasons. First, it offers an alternative avenue to investigating the object concept. This is particularly important given that the object displacement series by itself can lead to important underestimations of the skills under study – a point clearly made by the recent research on infant reasoning about the physical world.

Second, it also offers a way to investigate knowledge about objects and how they affect each other. Thus, knowing about arrested motion is not merely equivalent to knowing that objects continue to exist when they are out of sight. In addition, it suggests that individuals have some knowledge about the fact that objects take up space, and more importantly, about the influence that hidden objects may exert over visible ones. Only recently some studies have addressed these questions by investigating phenomena such as gravity and solidity in nonhuman animals (e.g., Hauser, 2001; Hood, Hauser, Anderson, & Santos, 1999; Santos & Hauser, 2002). The arrested motion paradigm can provide valuable information about what individuals know about object–object interactions and causal understanding – an area that has been traditionally dominated by studies on tool-use (e.g., Antinucci, 1989; Chappell & Kacelnik, 2002, 2004; Povinelli, 2000; Tebbich & Bshary, 2004; Visalberghi & Limongelli, 1994). It is

important that the view derived from tool-using studies in which the action on tools (with all the complexities that this already entails) is complemented by studies in which tools are eliminated from the equation. The simplicity of the arrested motion paradigm seems particularly suited to investigate the skills in a number of species.

In the current study, we investigated the arrested motion phenomenon in great apes. The basic procedure of this study owes much to the original Baillargeon et al. (1985) setup and the related unveiling experiments conducted afterwards (cited in Baillargeon, 1995). Yet, we adapted the paradigm both in the way we measured the individual responses and presented the stimuli. Instead of using looking measures, we used the tendency of primates to maximize their food intake by selecting baited containers as opposed to empty ones. In the initial experiment, we presented two identical boards on a platform. One of the boards had a piece of food under it so that it acquired an inclined orientation whereas the other remained flat on the platform. In follow-up experiments we investigated this phenomenon in detail by ruling out potential alternative explanations and exploring the limits of this skill in the great apes.

2. Experiment 1: static arrested motion

This first experiment assayed the general testing procedure and assessed whether apes are capable of using the inclined orientation of the board to find the reward.

2.1. Methods

2.1.1. Subjects
Six orangutans, 7 gorillas, and 4 bonobos housed at the Wolfgang Köhler Research Center, Leipzig Zoo (Germany) participated in this study. Table 1 presents the age, sex, rearing, and experimental participation of each subject. There were 10 females and 7 males ranging from 5 to 29 years of age. All apes were mother reared except for the three bonobo males who were nursery 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.

2.1.2. Materials
Two wooden boards ($25 \, cm \times 9 \, cm$) were placed on a wooden platform about $40 \, cm$ apart in front of a vertical Plexiglass partition with three equidistant circular holes ($6 \, cm$ in diameter) on its bottom part just above the platform. Subjects could use these holes to select one of the boards placed in front of the left and right holes. The center hole was used to deliver the reward to the subject. Two wooden cubes ($9 \, cm \times 6 \, cm \times 3.5 \, cm$) placed behind and under the boards kept them in an inclined orientation in the control trials (see below). Before the test started subjects were allowed to look at the boards and cubes. We used grapes and monkey chow as rewards.

2.1.3. Procedure and design

The experimenter (E) and the subject sat facing each other on either side of the Plexiglass partition, with the platform between them (on E's side). Subjects were accustomed to this procedure and quickly approached E and sat facing him as soon as he sat behind the platform. E placed the two boards on the platform while subjects watched and then raised an opaque screen to block visual access to the baiting process. Then, E showed the reward to the subject and placed it behind the opaque screen under/on one of the boards depending on the experimental condition. There were three experimental conditions (see Fig. 1):

2.1.3.1. Baseline. E placed the reward on top of one of the boards.

2.1.3.2. Inclined. E placed the reward under one of the boards so that from the point of view of the subject the baited board acquired an inclination of approximately 30°.

2.1.3.3. Control. E placed the reward under one of the boards but also placed a wooden cube under and behind each board so that both acquired an inclination of approximately 30°. From their perspective, subjects were able to see that the wooden cubes protruded from behind the center of each board. This condition assessed the possibility that subjects used inadvertent cues by the experimenter, the food, or the baiting procedure to find the food.

Table 1
Name, species, age, sex, rearing history, and the experiments in which each subject participated

| Name	Species	Age (years)	Sex	Rearing history	Experiment participation
Gorgo	Gorilla	21	M	Nursery	1–4
Bebe	Gorilla	24	F	Unknown	1
Ndiki	Gorilla	24	F	Unknown	1
Viringika	Gorilla	7	F	Mother	1–4
Vizuri	Gorilla	7	F	Mother	1
Nkwango	Gorilla	6	M	Mother	1–4
Ruby	Gorilla	5	F	Mother	1–4
Joey	Bonobo	20	M	Nursery	1
Ulindi	Bonobo	9	F	Mother	1–6
Limbuko	Bonobo	7	M	Nursery	1–6
Kuno	Bonobo	6	M	Nursery	1–6
Yasa	Bonobo	7	F	Mother	5, 6
Dunja	Orangutan	29	F	Unknown	1
Bimbo	Orangutan	22	M	Mother	1–6
Pini	Orangutan	14	F	Mother	1
Walter	Orangutan	13	M	Mother	1–4
Toba	Orangutan	8	F	Mother	1–4
Dokana	Orangutan	16	F	Unknown	5, 6
Padana	Orangutan	5	F	Mother	1
Alexandra	Chimpanzee	6	F	Nursery	6
Annett	Chimpanzee	6	F	Nursery	6
Alex	Chimpanzee	5	M	Nursery	6
Unyoro	Chimpanzee	9	M	Mother	6
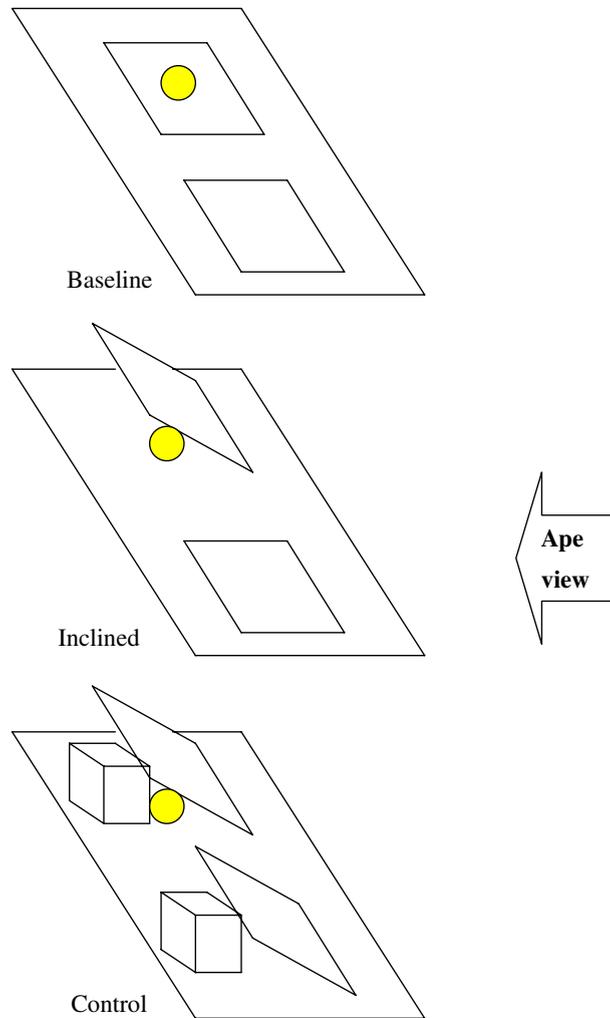
Fig. 1. Experimental conditions used in Experiment 1.

In half of the trials E placed the reward on/under the left board whereas in the other half E left the reward on/under the right side board. E always touched both boards in each trial to prevent subjects from using his arm movements as a cue for the location of food. After administering each of these conditions, E removed the opaque screen and pushed the platform against the Plexiglass partition so that the subjects could choose one of the boards. The first board touched by the subject was scored as his/her choice by the E. We did not assess inter-observer reliability because the subjects' choices were unambiguous.

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.
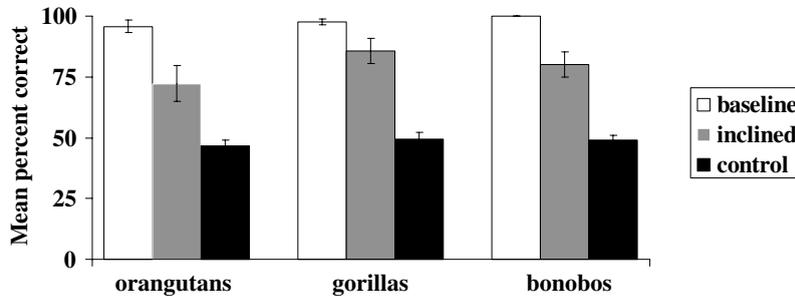
Fig. 2. Mean percentage (SEM) of correct trials across conditions for each species in Experiment 1.

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 the only two restrictions that it appeared the same number of times on each side and could not appear more than two times in succession on the same side.

2.2. Results

Fig. 2 presents the percentage of correct trials across conditions for each species. A species × condition ANOVA on the percentage of correct trials revealed a significant effect for condition, $F(2,28) = 94.94$, $P < 0.001$, and no effect for species, $F(2,14) = 2.16$, NS, or species × condition, $F(4,28) = 0.66$, NS. Post hoc analyses using the Bonferroni–Holm procedure (Holm, 1979) revealed that subjects performed better in the Baseline compared to the Inclined, $t(16) = 5.17$, $P < 0.001$ and Control conditions, $t(16) = 23.23$, $P < 0.001$. More importantly, subjects also performed significantly better in the Inclined compared to the Control condition, $t(16) = 7.12$, $P < 0.001$. Moreover, subjects performed above chance (50% correct) in the Baseline, $t(16) = 44.22$, $P < 0.001$ and Inclined conditions, $t(16) = 8.14$, $P < 0.001$. Even if one focused on the first four trials of the Inclined condition, subjects still performed above chance (mean = 75%, SEM = 6.1, $t(16) = 4.12$, $P = 0.001$).

Individual analyses indicated that all subjects were above chance in the Baseline condition (Binomial test: $P < 0.05$). Additionally, five (out of 7) gorillas, three (out of 4) bonobos, and three (out of 6) orangutans were above chance in the Inclined condition (Binomial test: $P < 0.05$). In contrast, no subject was above chance in the Control condition (Binomial test: NS). To analyze any potential learning effects we compared the subjects' performance across 6-trial blocks in the Inclined condition. There was no change in performance across blocks of trials, $F(3,48) = 0.25$, NS.

2.3. Discussion

Subjects preferentially selected the baited board in the Inclined condition, but not in the Control condition. Since the same baiting procedure, food odours, and the experimenter's behavior (including the potential inadvertent cues that he may have provided) were present in both conditions, it is very likely that subjects used the

differential orientation of the boards to select the correct alternative in the Inclined condition.

There were no species differences in performance. In contrast, there were important individual differences. While some subjects mastered the task, others remained at chance levels throughout testing. Moreover, there was no evidence that subjects learned to select the inclined board during testing. In the next experiment we further explored the nature of this knowledge by presenting a harder version of the same problem.

3. Experiment 2: two inclined boards

This experiment investigated whether subjects were able to solve a harder problem. In the critical condition we presented two inclined boards. One board owed its inclination to a reward placed under it (same as the Inclined condition of Experiment 1) whereas the other board owed its inclination to a visible support (same as the Control condition of Experiment 1). Thus, although both boards could potentially hide the reward, the reasons for their inclination differed. Whereas the inclination of the unsupported board could only be due to the presence of the reward, the inclination of the supported board could be due either to the reward or the wood support.

3.1. Methods

3.1.1. Subjects
All subjects that were above chance in the Inclined condition of Experiment 1 except the gorilla Vizuri, which was not available at the time of testing, participated in this study (see Table 1). These were four gorillas, three orangutans, and three bonobos.

3.1.2. Materials
The same two wooden flat boards and rewards used in Experiment 1. We also used two larger wooden supports (25 cm × 6 cm × 3 cm) to enhance their visibility.

3.1.3. Procedure and design
The general procedure was identical to that of Experiment 1. E placed the two boards on the platform, raised the opaque screen, showed the reward to the subject and placed it under/on one of the boards depending on the experimental condition. There were three experimental conditions:

3.1.3.1. Baseline. Same as Experiment 1.

3.1.3.2. Inclined-block. E placed the reward under one of the boards so that it acquired the same slope as in the Inclined condition of Experiment 1. Then, E placed the wooden support behind the other board so that it also acquired the same inclination as in the Control condition of Experiment 1. Thus, both boards displayed a 30° inclination
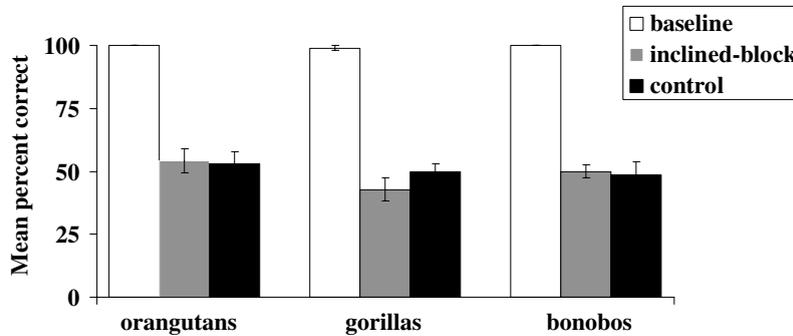
Fig. 3. Mean percentage (SEM) of correct trials across conditions in Experiment 2.

approximately and subjects were able to see that one of the boards rested on the wooden support, which protruded from behind the board from the subject's perspective.

3.1.3.3. Control. Same as Experiment 1.

Each subject received three 24-trial sessions for a total of 24 trials per condition. The randomization procedures and restrictions for administering the various conditions and reward position were identical to those of Experiment 1.

3.2. Results

Fig. 3 presents the percentage of correct trials across conditions for each species. A species × condition ANOVA on the percentage of correct trials revealed a significant effect for condition, $F(2,14) = 312.84$, $P < 0.001$, and no effect for species, $F(2,14) = 0.97$, NS, or species × condition, $F(4,14) = 1.28$, NS. Post hoc analyses using the Bonferroni–Holm procedure revealed that subjects performed better in the Baseline compared to the Inclined-block, $t(9) = 18.90$, $P < 0.001$ and Control conditions, $t(9) = 22.13$, $P < 0.001$. In contrast, there was no significant difference between the Inclined-block and the Control condition, $t(9) = 1.00$, NS. Moreover, subjects performed above chance (50% correct) in the Baseline, $t(9) = 119.0$, $P < 0.001$, but not in the Inclined-block, $t(9) = 0.61$, NS, or Control conditions, $t(9) = 0.19$, NS.

Individual analyses indicated that all subjects were above chance in the Baseline condition (Binomial test: $P < 0.05$). In contrast, no subject was above chance in the Inclined-block or Control conditions (Binomial test: NS).

3.3. Discussion

Subjects failed to take into account the source of the inclination. In retrospect, this is a much harder problem than the one presented in Experiment 1 because, strictly speaking, there is no reason that would prevent the reward from being under the board that was inclined due to the presence of the wooden support. So, unlike Experiment 1 in which there was a clear and absolute difference between the flat and the inclined boards (and the food could not be under the flat board), this was not the case in the current

test, because it was still possible for the food to be under any of the two inclined boards. However, subjects could have solved the problem if they had considered the food as the only reason for the inclination of the board without a protruding block.

One potential problem for this experiment is that the presence of two inclined boards may have been distracting to the subjects and they may have decided after an initial inspection that the problem was unsolvable. This may be especially true given that control conditions in previous experiments invariably consisted of two equally inclined boards. We conducted the next experiment to test this possibility and presented two boards that were initially inclined and then one of them changed its orientation. This test also approximated the original arrested motion experiment (Baillargeon et al., 1985) in which the screen rotated 180° until it stopped flat on the table while the other stopped at the point in which it seemingly reached the object located behind it. The question was whether subjects would be able to take into account this more dynamic information to solve the problem.

4. Experiment 3: dynamic arrested motion

In this experiment we returned to the initial problem of having an inclined (i.e., baited) and a flat board on the platform at the time of choice. However, before subjects experienced this display, they were presented with two equally inclined boards – one of which fell flat on the platform (while the other remained inclined) during the course of the trial and before subjects were allowed to choose. Thus, although initially both boards could potentially hide the reward, this changed after one of the boards fell flat on the platform. Solving this problem would mean that subjects can update information regarding the presence of the reward.

4.1. Methods

4.1.1. Subjects
Same as Experiment 2.

4.1.2. Materials
The same two wooden flat boards, wooden supports, and rewards used in Experiment 1.

4.1.3. Procedure and design
The general procedure was identical to that of Experiment 1. E placed the two boards on the platform, raised an opaque screen, showed the reward to the subject and placed it under/on one of the boards depending on the experimental condition. There were three experimental conditions:

4.1.3.1. Baseline. Same as Experiment 1.

4.1.3.2. Inclined-dynamic. E placed the reward under one of the boards and the support behind each board so that both acquired a 30° inclination. This was the same

setup as the Control condition in Experiment 1. After E removed the opaque screen, E let the subject watch both inclined boards and then pushed them simultaneously (from the top and behind) towards the subject so that they fell off their respective supports. This resulted in the baited board remaining in an inclined orientation whereas the other board fell flat on the platform.

4.1.3.3. Control. Same as Experiment 1.

Each subject received three 24-trial sessions for a total of 24 trials per condition. The randomization procedures and restrictions for administering the various conditions and reward position were identical to those of Experiment 1.

4.2. Results

Fig. 4 presents the percentage of correct trials across conditions for each species. A species × condition ANOVA on the percentage of correct trials revealed a significant effect for condition, $F(2, 14) = 50.96$, $P < 0.001$, and no effect for species, $F(2, 14) = 3.30$, $P = 0.096$, or species × condition, $F(4, 14) = 1.43$, NS. Post hoc analyses using the Bonferroni–Holm procedure revealed that subjects performed better in the Baseline compared to the Inclined-dynamic, $t(9) = 3.32$, $P = 0.009$ and Control conditions, $t(9) = 10.70$, $P < 0.001$. There was also a significant difference between the Inclined-dynamic and the Control condition, $t(9) = 5.48$, $P < 0.001$. Moreover, subjects performed above chance (50% correct) in the Baseline, $t(9) = 37.97.0$, $P < 0.001$, and Inclined-dynamic conditions, $t(9) = 6.99$, $P < 0.001$ (first four trials: mean = 82.5%, SEM = 6.5, $t(9) = 4.99$, $P < 0.001$), but not in the Control condition, $t(9) = 1.27$, NS.

Individual analyses indicated that all subjects were above chance in the Baseline condition (Binomial test: $P < 0.01$). In addition, three (out of 4) gorillas, one (out of 3) orangutan, and all three bonobos were above chance in the Inclined-dynamic condition (Binomial test: $P < 0.01$). In contrast, no subject was above chance in the Control condition (Binomial test: NS).
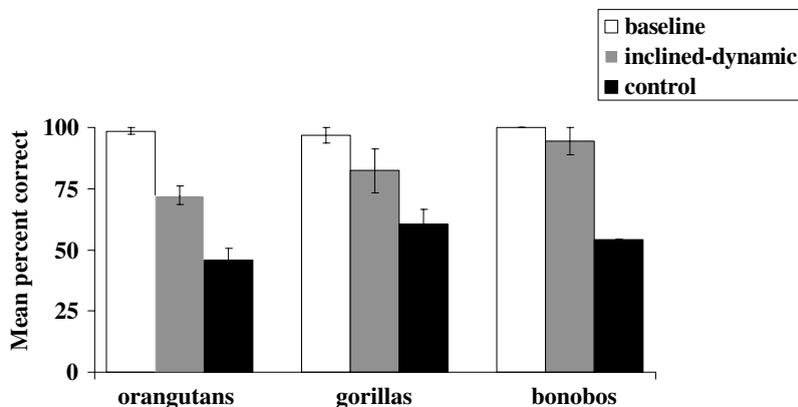

Fig. 4. Mean percentage (SEM) of correct trials across conditions in Experiment 3.

4.3. Discussion

Subjects performed at high levels in the Inclined-dynamic condition, thus replicating the results of Experiment 1 under more dynamic conditions. Furthermore, the results suggest that subjects updated their knowledge about the location of the reward in the course of the trial, or at least made their choices based on the information provided in the last part of the trial. Therefore, the negative results of the previous experiment cannot be explained as a fixation on the initial inclination of the boards. In the next experiment we turned our attention again toward another aspect of the problem by varying the size of the reward. Studies with human infants have shown that they can use the size of the occluder to decide if the object can be hidden by it. For instance, Baillargeon and DeVos (1994) have shown that 13-month-old infants are surprised when large objects are extracted from under cloths exhibiting a small protuberance. Similarly, Baillargeon (1991) have found that 6-month-old infants can detect violations of the angle at which the screen stops, which is a function of the size of the object that is behind the screen.

We tested this possibility in the apes by having two rewards of different sizes under two identical boards that acquired different inclinations depending on the object that what located under it. So the idea was to see if subjects would select the board with the steepest inclination since it was the one with the larger reward. We are able to use this procedure because several studies have shown that apes prefer to take larger of two solid or liquid food quantities (Boysen & Berntson, 1995; Call, 2000; Dooley & Gill, 1977; Suda & Call, 2004).

In addition to the size of the reward, we investigated another aspect: the quality of the reward. We manipulated the size and the quality of the reward simultaneously because both size and quality of the reward are responsible for the subjects' choices. This joint assessment allowed us to investigate whether subjects were sensitive to the kind of food that was responsible for the inclination of the food rather than just responding to the size of the reward.

5. Experiment 4: size of the reward

In this experiment each board showed a different inclination that corresponded to the size of the reward that was hidden under it. So unlike previous studies, there were always two pieces of food of different sizes in each trial and subjects had to select one of them. In half of the trials the large reward was a piece of a highly preferred food (i.e., banana) and the small reward was a piece of a less preferred food (i.e., carrot). In the other half of the trials the large reward was a piece of the less preferred food and the small reward was a piece of the highly preferred food. Before hiding each reward under a board, subjects were allowed to observe the pair of rewards that would be used in that particular trial. Since apes prefer even small banana pieces to large carrot pieces, the idea was whether subjects would select the more inclined board when there was a large banana piece in the trial and the less inclined board when there was a small banana piece in the trial. In addition, we also conducted a Baseline condition in which we checked the preference for the various combinations of foods and a control condition as in previous experiments.

5.1. Methods

5.1.1. Subjects
Same as Experiment 3.

5.1.2. Materials
The same two wooden flat boards and wooden supports used in Experiment 1. We used banana and carrot pieces cut in two different sizes: large (4–5 cm) and small (1–2 cm). The small reward under the board produced an inclination of approximately 25° whereas the large reward produced an inclination of approximately 45°.

5.1.3. Procedure and design
The general procedure was similar to Experiment 1 except that there were two rewards instead of just one. E placed a pair of rewards on the platform for the subject to see. There were two types of reward pairs depending on the size and the type of reward: large banana with small carrot (LB–SC) and small banana with large carrot (SB–LC). After subjects had looked at the rewards, E raised an occluding screen and placed each of them in an upright position under/on one of the boards depending on the experimental condition. There were three experimental conditions (see Fig. 5):
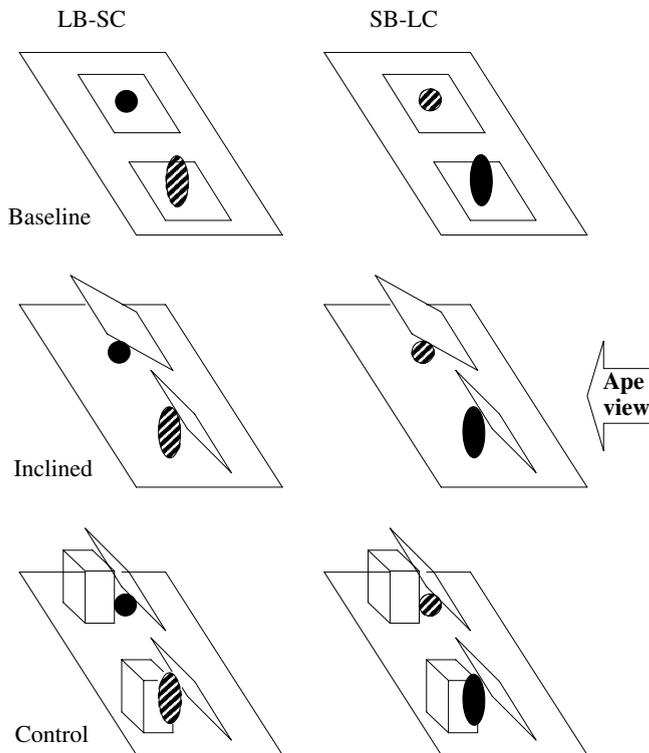

Fig. 5. Experimental conditions used in Experiment 4.

5.1.3.1. Baseline. E placed one reward on each board.

5.1.3.2. Inclined-size. E placed one reward under each board so that both boards acquired an inclined orientation that differed according to the size of the reward that it occluded. The small reward created a 25° slope while the large reward created a 45° slope.

5.1.3.3. Control. E placed one reward under each board as before but also the support behind each board so that they acquired the same inclination, which corresponded to the inclination of the larger reward (45°). This condition assessed the possibility that subjects used inadvertent cues by the experimenter, the food, or the baiting procedure to find the food.

Each subject received three 24-trial sessions for a total of 24 trials per condition. Half of the trials used the large banana with small carrot (LB–SC) combination while the other half used the small banana with large carrot (SB–LC) combination. The randomization procedures and restrictions for administering the various conditions and reward position were identical to those of Experiment 1.

5.2. Results

Fig. 6 presents the percentage of trials in which subjects selected the banana piece across conditions for each species in each of the two reward combinations. Focusing first on the LB–SC trials (see Fig. 6a), a species × condition ANOVA revealed a significant effect for condition, $F(2, 14) = 68.56$, $P < 0.001$, species × condition, $F(4, 14) = 4.26$, $P = 0.018$, but no main effect for species, $F(2, 7) = 2.92$, NS. Post hoc analyses using the Bonferroni–Holm procedure indicated that subjects performed better in the Baseline compared to the Inclined-size, $t(9) = 3.45$, $P = 0.007$ and Control conditions, $t(9) = 17.67$, $P < 0.001$. There was also a significant difference between the Inclined-size and the Control condition, $t(9) = 4.20$, $P = 0.002$. Moreover, subjects preferentially selected LB over the SC in both the Baseline, $t(9) = 26.71$, $P < 0.001$, and Inclined-size conditions, $t(9) = 4.74$, $P = 0.001$ (first four trials: mean = 80.0%, SEM = 11.1, $t(9) = 2.71$, $P = 0.024$), but not in the Control condition, $t(9) = 1.31$, NS. Analyzing the species separately, revealed no significant differences between the Baseline and the Inclined-size conditions for any species (all t-tests $P > 0.05$) whereas there was a significant difference between the Inclined-size and the Control condition for gorillas, $t(3) = 3.66$, $P = 0.035$ and bonobos, $t(2) = 5.29$, $P = 0.034$, but not for orangutans, $t(2) = 0.76$, NS.

Focusing on the SB–LC trials (see Fig. 6b), a species × condition ANOVA revealed a significant effect for condition, $F(2, 14) = 27.96$, $P < 0.001$, and no effect for species, $F(2, 7) = 2.1$, NS, or species × condition, $F(4, 14) = 1.15$, NS. Post hoc analyses using the Bonferroni–Holm procedure indicated that subjects performed better in the Baseline compared to the Inclined-size, $t(9) = 6.58$, $P < 0.001$ and Control conditions, $t(9) = 3.94$, $P = 0.003$. There was also a significant difference between the Inclined-size and the Control condition, $t(9) = 3.85$, $P = 0.004$. Moreover, subjects preferentially selected SB over the LC in the Baseline condition, $t(9) = 3.74$, $P = 0.005$. In contrast, subjects preferentially selected the LC over SB in the Inclined-size condition,
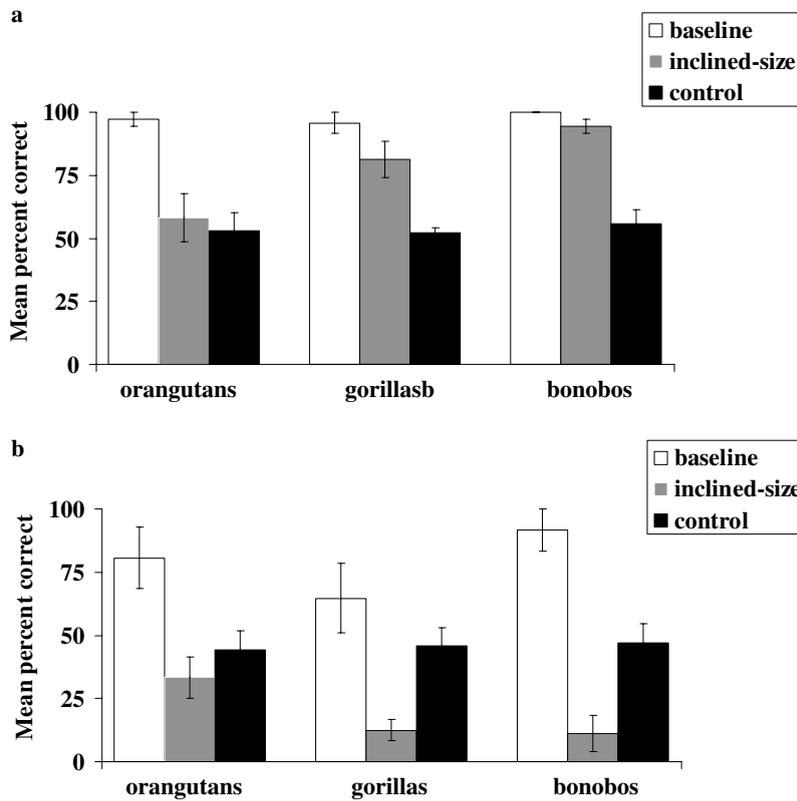
Fig. 6. Mean percentage (SEM) of correct trials across conditions in Experiment 4 for the (a) large banana–small carrot and the (b) small banana–large carrot trials.

$t(9) = 6.86$, $P = 0.001$ (first four trials: mean = 75.0%, SEM = 8.3, $t(9) = 3.0$, $P = 0.015$). Finally, subjects showed no preference for the LC or SB in the Control condition, $t(9) = 1.10$, NS.

Individual analyses indicated that seven out of 10 subjects selected the board with the steepest slope above chance levels in the Inclined condition (Binomial test: $P < 0.05$). Eight out of 10 subjects preferentially selected the banana in the Baseline condition (Binomial test: $P < 0.05$). In contrast, no subject was above chance in the Control condition (Binomial test: NS).

5.3. Discussion

Bonobos and gorillas preferentially selected the board with the steepest inclination on both types of trials, probably because they tried to obtain the larger piece of food. This suggests that they can use the relative inclination of the board to maximize their food intake, thus replicating and extending the results from previous experiments. In doing so, however, they failed to take into account that picking the steepest board in

the SB–LC trials meant receiving the large carrot, which they had not preferred in Baseline trials, in which they preferred choosing the small banana piece instead. Orangutans were less likely to use the differential inclination of the boards to select the largest food. This was particularly true in the LB–SC condition. However, this lack of preference for size did not translate into a preference for the banana in the Inclined-size condition regardless of the size of the reward. Thus, these data seems to suggest that subjects, particularly bonobos and gorillas, took the size of the reward into account but not the type of reward that was hidden under the board.

One possible explanation for these negative results is that subjects had difficulty coping with two types of information (quality and quantity). The large size meant more quantity but it meant lower quality when it represented the carrot. In fact, studies with infants have shown that presenting a 'reminder' of the original size of the occluded object (by placing next to the object to be occluded an object of the same size) improved the performance of 41/2-month-old infants (Baillargeon, 1991, 1995). In the next experiment, we re-tested the SB–LC condition but provided subjects with a reminder of the type of hidden food.

6. Experiment 5: size of the reward with a reminder

In the previous experiment subjects showed a marked preference for the small banana over the large carrot when both were visible (Baseline condition). However, this preference disappeared when the rewards were located under the boards (Inclined-size condition). Thus, subjects appeared not to use the differentially inclined boards to locate the small banana piece. In this experiment we provided subjects with additional information regarding the type of reward that was hidden under each board to see if their performance would improve. In particular, we placed a small banana and a large carrot piece in the center of the platform between the two inclined boards to see if they could use this information to decide between the two boards displaying different slopes. We also administered the inclined condition (SB–LC) used in the previous experiment to directly compare both versions of the task and the baseline condition to check that they still preferred the small banana over the large carrot.

6.1. Subjects

All subjects included in Experiment 4 and that were available at the time of testing participated in the current experiment. In addition, we tested one 7-year-old bonobo female and one 16-year-old orangutan female that had not participated in the previous experiments. Thus, we tested a total of four bonobos and two orangutans (see Table 1).

6.2. Materials

Same as those used in Experiment 4 except that we only used reward pairs composed of small banana and large carrot pieces.

6.3. Procedure and design

The general procedure was identical to Experiment 4 in which subjects had to choose one of two boards concealing different rewards and displaying different slopes. There were three conditions:

6.3.1. Baseline
Same as Experiment 4.

6.3.2. Inclined-size
Same as Inclined-size (LC–SB) condition in Experiment 4.

6.3.3. Reminder
Same as the previous condition except that the E placed two pairs of rewards (instead of just one) on the center of the platform between the two flat boards. The two large carrots were at the back and the two small bananas in front. Then, E raised the opaque screen and placed one of the two pairs of rewards under the boards. After the E removed the occluder, subjects saw the differentially inclined boards and the remaining reward pair on the center of the platform. The visible pair was located between the inclined boards forming a straight line with the rewards hidden under each board. In order not to bias subjects for one side due to the presence of one type of visible reward, the visible banana was always placed in front (not to the side) of the visible carrot (from the subject's perspective).

Each subject received two 16-trial sessions. Each session consisted of 4 Baseline trials to assess their preference for the types of rewards used during the experiment and 12 trials of one of the other two conditions with the order of presentation for each condition counterbalanced across subjects and reward position counterbalanced within subjects.

6.4. Results

Similar to Experiment 4, subjects' preference for the small banana piece varied significantly across conditions, $F(2, 10) = 33.06$, $P < 0.001$ (Fig. 7). They preferred the small banana to the large carrot in 95.8% of the trials in the Baseline condition, $t(5) = 17.39$, $P < 0.001$. Additionally, post hoc analyses using the Bonferroni–Holm procedure indicated subjects selected the banana significantly more often in the Baseline compared to the Inclined-size and Reminder conditions ($P < 0.005$). Unlike Experiment 4, however, they selected the banana in the Inclined-size condition in 45.8% of the trials, which is not significantly different from chance, $t(5) = 0.66$, NS. Also, contrary to our expectation, there was no improvement in performance in the Reminder condition compared to the Inclined-size condition ($P = 0.34$). Subjects selected the banana in the Reminder condition in 38.9% of the trials, which again is not significantly different from chance, $t(5) = 1.45$, NS.
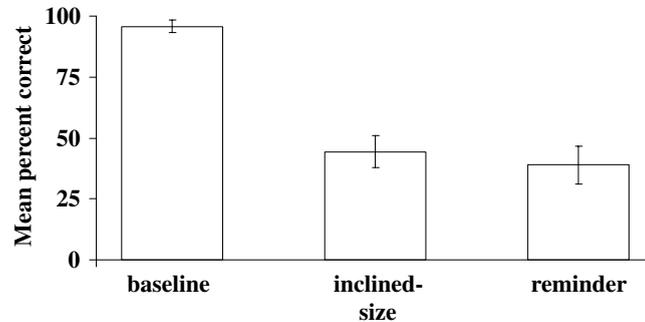
Fig. 7. Mean percentage (SEM) of correct trials across conditions in Experiment 5.

Individual analyses indicated that only one out of six subjects selected the board with the steepest slope above chance levels in the Inclined-size and Reminder conditions combined (Binomial test: $P < 0.05$). Four out of six subjects selected the banana above chance levels in the Baseline condition (Binomial test: $P < 0.05$).

6.5. Discussion

We found no evidence that 'reminding' subjects of the kind of hidden rewards (by presenting them with an identical pair of rewards at the time of choice) helped subjects to select the small banana piece above chance levels. Our small sample size precluded us from comparing those subjects that received the Reminder condition first with those that received it second to see if reminding had a significant effect on the subjects' choices. Nevertheless, subjects still showed a preference for the board with the greater inclination in the same direction as in Experiment 4. However, the overall the preference for the board with the larger inclination had substantially declined compared to Experiment 4. One possible explanation for these results is that repeated testing made subjects realize that in order to get the banana, subjects had avoid selecting the board with the largest inclination, which seemed to have been their natural tendency. This agrees with data on reverse contingency research showing that apes can learn to select the smaller of two quantities to net the larger one (e.g., Shumaker, Palkovitch, Beck, Guagnano, & Morowitz, 2001; Vlamings, Uher, & Call, 2006).

Nevertheless, the decline in the tendency to select the board with the larger inclination in the hidden condition might have indicated that our initial results could not be consistently replicated. Such results might also weaken the argument that apes attributed a causal role to the reward in creating the sloped orientation of the board. Therefore, we decided to run three final conditions to see if we could replicate our original results and to test whether naïve apes showed a preference for an inclined board independent of the causal role that the reward may have played in causing such orientation.

7. Experiment 6: replication and control tests

In the first condition we presented subjects with the Inclined condition of Experiment 1 to assess whether they still preferred an inclined board (caused by the presence of the reward) compared to a flat board. The second condition assessed whether subjects preferred a board with the largest inclination (out of two inclined boards). Unlike the condition used in Experiment 4, both inclined boards harboured the same type of food (e.g., banana) that differed in size. The third condition investigated whether naïve individuals preferred objects with inclined surfaces independently of whether the presence of the reward caused the inclination. Thus, we presented four naïve chimpanzees with a platform that had one hole drilled on each side so that a reward could be placed inside them. Each hole was covered either with either a flat board or a wedge, which produced the same perceptual appearance as a board that had a reward under it. Crucially, in this test the reward, which was always located inside the hole under the wedge, had no effect on the orientation of the wedge. If subjects simply preferred objects with inclined surfaces they should select the wedge over the flat board. Additionally, they should perform at the same level as those subjects tested in Experiment 1.

7.1. Methods

7.1.1. Subjects
We tested all subjects that had participated in Experiment 5 (2 orangutans and 4 bonobos) and four chimpanzees that had no prior experience with this paradigm (see Table 1). The experienced apes participated in the Inclined and Inclined-relative conditions whereas the naïve apes participated in the Wedge condition.

7.1.2. Materials
There were two pairs of objects. A pair of identical green rectangular boards (24 cm × 10 cm) that had two of their corners on the same side cut in a curved fashion were used to administered the Inclined and Inclined-relative conditions. When placed on the platform, the side with the cut corners was closest to the experimenter. The reason for the novel color and shape of the boards was to make them as distinct as possible from other boards that subjects had encountered in previous experiments.

The second pair of objects was used in the Wedge condition and consisted of one of the boards used in Experiment 1 and a solid wooden wedge (25 cm × 8 cm × 3.5 cm) that when placed on the platform with its sloped side facing the subject closely resembled an inclined baited board from Experiment 1. In this condition, we also replaced the flat platform from previous experiments by one with one hole on each side where the reward could be introduced. This meant that the reward had no effect on the orientation of the boards that were placed on top of the holes.

We used slices of banana, grapes, or pieces of monkey chow (1–2 cm in size) for the Inclined and Wedge conditions and banana and carrot pieces cut in two different sizes (large: 4–5 cm; small: 1–2 cm) in the Inclined-relative condition.

7.1.3. Procedure

The same basic procedure as in previous experiments was followed. A reward was placed on the platform, the experimenter raised a screen that prevented the subject's visual access and then placed the reward under one of the two boards. Subjects could select one of the objects by touching it. There were three conditions:

7.1.3.1. Inclined. Same as Experiment 1.

7.1.3.2. Inclined-relative. Same as the Inclined-size condition of Experiment 4 except that within each trial we varied the size of the reward but not its type. Thus, subjects were shown either two pieces of banana (one large and one small) or two pieces of carrot (one large and one small) that were then hidden under each of the boards.

7.1.3.3. Wedge. We presented the objects on the platform with holes. Before the test began, subjects were first allowed to inspect the holes in the platform by dropping one reward inside of each of them that the experimenter retrieved and gave to the subject. They were also shown the wedge and the flat board from different angles so that they could visually inspect them. Then, the experimenter began the test by raising the screen, depositing the reward inside one of the holes and covering it with the wedge. The other hole was covered with the flat board. While depositing the reward, the experimenter moved his hand and touched both holes to prevent subjects from using the experimenter's arm movements to determine where the reward had been deposited.

Each subject received one 12-trial session in each condition. In the Inclined-relative condition, half of the subjects received the first six trials with banana pairs and the next six trials with carrot pairs. The order of presentation for banana and carrot was reversed for the other half of the subjects. We analyzed the data in the same way as in previous experiments.

7.2. Results and discussion

Subjects showed a strong preference for the inclined over the flat board (Inclined condition, Fig. 8), $t_5 = 5.32$, $P = 0.003$. Additionally, subjects also preferred the board with the larger inclination compared to the one with the smaller inclination (Inclined-relative condition, Fig. 8), $t_5 = 8.70$, $P < 0.001$. There were no significant differences between banana pairs and carrot pairs, $t_5 = 0.50$, NS. Individual analyses indicated that four out of six subjects selected the slopped board above chance levels in the Inclined condition (Binomial test: $P < 0.05$). Two out of six subjects also selected the board with the steepest slope in the Inclined-relative condition above chance levels (Binomial test: $P < 0.05$). Thus, the current experiment replicated previous results.

In contrast, naïve chimpanzees showed no preference for the wedge, $t_3 = 0.43$, NS (Wedge condition, Fig. 8). In fact, their preference for the wedge was significantly lower than the preference for the inclined board shown by subjects in Experiment 1, $t_{19} = 2.88$, $P = 0.01$. Such a difference is remarkable because the reward was located under both objects and they had a very similar appearance when resting on the
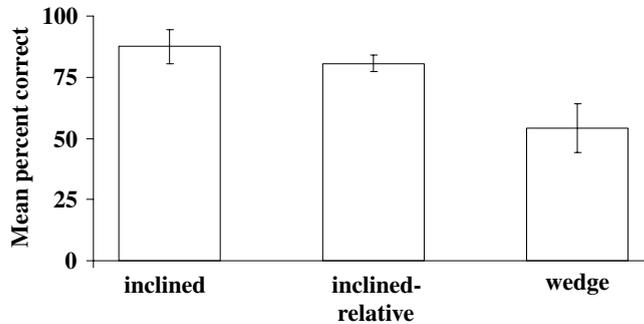
Fig. 8. Mean percentage (SEM) of correct trials across conditions in Experiment 6.

platform. Moreover, subjects got rewarded every time they selected the wedge, but still they did not show a preference for it. Individual analyses indicated that no subject was above chance in the Wedge condition (Binomial test: NS). This means that subjects showed no default preference for inclined objects over flat ones, reinforcing the idea that the preference for the inclined board had to do with effect that the reward had on the board.

7.3. General discussion

Apes were able to locate a food reward based on the degree of inclination of one of two boards placed on a platform. This result confirms previous studies showing that subjects understand that food continues to exist even if it is not directly perceived. More importantly, it also suggests that apes know that the presence of solid objects can affect the orientation of other objects in space, and they can use such information to infer the location of food. In addition, this study produced two other results.

First, apes also performed well in the arrested motion task under more dynamic conditions. This means that they were able to adjust their choices depending on the most recent information they acquired, and were not fixed by the first display that they saw. This result is reminiscent of the arrested motion findings of Baillargeon et al. (1985, see also Baillargeon, 1991) with young infants. Second, apes can use the relative inclination of the board to find the larger of two food rewards. This result parallels those of children using the relative size or orientation of an occluder to assess whether a given object can be effectively hidden under that particular object (Baillargeon, 1991, 1995). Moreover, the apes' preference for the steeper of two boards cast some doubt over the interpretation that apes solved the initial experiments simply because they preferred inclined over flat surfaces. To account for the results of Experiments 1, 3, and 5 one would have to postulate that apes not only preferred inclined over flat surfaces, but also steeper over less steep ones. An alternative to this 'fixed' preference for inclined surfaces is that subjects selected the steepest surface to net the largest piece of food. This would suggest that subjects are capable of making a direct connection between the orientation of the visible object (the board) and its hidden cause (the food).

There are two additional pieces of evidence suggesting that apes may indeed have some knowledge regarding the connection between the hidden object and the inclined orientation of the board. First, naïve individuals showed no preference for objects with inclined surfaces when the reward did not cause their inclination (wedge test, Experiment 6). This finding contrasts dramatically with the preference shown in Experiment 1 in which the reward caused the orientation. Second, we tested the same subjects included in the current study in traditional color and shape discrimination problems (Call, 2006). The general procedure was comparable to that used in the current study: subjects had to select between two alternative objects placed on a platform and they were rewarded if they selected the correct object. Their performance on these simple discrimination tasks was consistently inferior to their performance on the arrested motion task or other tasks in which subjects had to infer the presence of a reward by the noise it would have made if it had been inside a container that the experimenter shook (Call, 2004). One possible explanation for this difference is that apes perform better in problems grounded on logico-causal compared to arbitrary relations (Call, 2004, 2006; Premack, 1995).

Despite these positive results, there are two aspects of this task for which we failed to find positive evidence. First, apes ignored information that was not directly linked with the reward that would have helped them to dismiss one of the boards as a less likely alternative for the location of food. In particular, in Experiment 2 they did not take into account that the piece of wood behind the board could explain its inclination, thus opening the possibility that the board without the wooden block behind it, yet inclined, was the board that hid the reward. Clearly, this is a harder problem than one flat board compared to an inclined one (Experiment 1) because the flat board *cannot* harbor the reward under it. In contrast, if the board is supported by a piece of wood, it is still logically possible that the food may be under the board that is supported by the piece of wood. In fact, subjects had encountered this situation before in the control trials of the previous experiments. One intriguing possibility is that an excessive reliance on their logico-causal framework may have led them to perform poorly in this experiment. This 'overcorrection' could be analogous to the 'logical' mistakes that infants and children make in gravity or Piagetian conservation tasks (Piaget & Inhelder, 1969; Spelke, Breinlinger, Macomber, & Jacobson, 1992). It is also conceivable that the inclusion of an additional object such as the support, may have increased the computational complexity of the problem.

Second, although apes selected the board with the steepest inclination in Experiment 4 (and Experiment 6), they failed to take into account the quality of the reward that was hidden under each board. This was true even when they were 'reminded' in the last experiment of the types of rewards hidden. We can rule out that the size of the reward is a more salient feature than the quality of the reward because subjects preferred small bananas to large carrots (and large bananas to small carrots) when both were visible. We can also rule out that subjects in general are not able to encode size or quality of the reward since previous studies show that they can do both (e.g., size: Call, 2000; quality: Premack & Premack, 1994). Another question is whether they can also combine the representations that have been acquired independently, particularly when they belong to two different modalities. There is evidence showing

that they can combine representations about quantities when they belong to the same modality (e.g., Beran, 2001; Boysen & Berntson, 1989). However, one may speculate that apes may have more difficulty combining representations of disparate modalities. For instance, Call (2003) found that chimpanzees and orangutans were able to perform the two following tasks: (1) track the displacement of a reward under a cup after subjects had been shown the reward in its initial position, and (2) use the presence of an object (i.e., marker) on the cup to locate the food once the marker had been removed from the cup. The first task entailed forming a representation of the reward once it was covered by the cup and updating its position throughout the various displacements. The second task entailed forming a representation of the marker as an index for the location of the reward. Although subjects were proficient at both tasks separately, they had great difficulty combining both tasks to be able to track the reward's displacement whose initial location had been indicated by the presence of the marker (not by showing the actual reward) before the movement took place.

It is possible that subjects failed to take into account the quality of the reward because the size of the reward was 'directly' perceived through the board inclination whereas the quality of the reward was only indirectly related to size when both rewards were presented to the subject before the experimenter hid them under the boards. To remedy this situation, we presented subjects with a 'reminder' of the rewards that were hidden under the boards. Although this modification attenuated the subjects' preference for the board with the steepest slope shown in Experiments 4, it did not produce a preference for the board with the shallower orientation (harbouring the banana) comparable to the subjects' preference for the banana in the baseline condition. This result contrasts with studies with children that have shown that presenting a 'reminder' of the original size of the occluded object improved the performance of 41/2-month-old infants who would otherwise failed to detect large violations in the arrested motion task (Baillargeon, 1991, 1995). In contrast, by 6 months of age, infants are capable of representing the size of the occluded object and use this representation to estimate the point at which a rotating screen coming into contact with the object will stop (Baillargeon, 1995).

There are at least two factors that may have contributed to the inability of apes (compared to infants) to use the cue provided by the 'reminder'. First, it is conceivable that apes tend to rely more on spatio-temporal compared to feature information. Haun, Call, Janzen, and Levinson (2006) found that apes privileged spatial over feature information when searching for rewards hidden under containers. Second, it is very likely that presenting two different objects hidden under two different occluders increased the task difficulty. Indeed, Mareschal and Johnson (2003) found that young infants who can use feature or spatial information in occlusion tasks, experience difficulty when they have to maintain and integrate both types of information during occlusion events – a difficulty that is further increased in reaching compared to looking tasks (Mareschal, Plunkett, & Harris, 1999).

In conclusion, apes made inferences about the location of food based on the differential spatial orientation of objects. This study suggests that apes not only understand that objects continue to exist after undergoing a visual occlusion, but also take into account the effect that hidden objects may have on visible ones. It is hypothe-

sized that success in this task reveals the operation of a logico-causal cognitive process, and not merely the association of a certain orientation with the presence of the reward.

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