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Piagetian Liquid Conservation in the Great Apes (*Pan paniscus*, *Pan troglodytes*, and *Pongo pygmaeus*)

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An understanding of Piagetian liquid conservation was investigated in 4 bonobos (*Pan paniscus*), 5 chimpanzees (*Pan troglodytes*), and 5 orangutans (*Pongo pygmaeus*). The apes were tested in the ability to track the larger of 2 quantities of juice that had undergone various kinds of transformations. The accuracy of the apes' judgment depended on the shape or number of containers into which the larger quantity was transferred. The apes made their choice mainly on the basis of visual estimation but showed modest success when the quantities were occluded. The results suggest that the apes rely to a greater extent on visual information, although they might have some appreciation of the constancy of liquid quantities.

Liquid conservation refers to the ability to understand that liquid quantities remain constant despite transformations in appearance. This ability is considered as an important step toward the formation of logical thinking in children because it shows that individuals appreciate the identity principle, that is, objects' physical properties remain constant even when their appearance changes (Piaget, 1941/1997). Piaget and Inhelder (1941) devised a number of tasks to examine whether children were capable of conserving quantities after a variety of perceptual transformations. In the classic liquid conservation experiment, a child is presented with two identical beakers filled with the same amount of water. After the child recognizes that the quantities are equal, the contents of one of the containers are poured into a new beaker, which is either narrower or wider, therefore leading to a different appearance. Alternatively, one of the quantities is equally divided into several small beakers. Children begin to successfully pass the liquid conservation test at around 7–8 years of age (Piaget & Inhelder, 1966/1969).

In the field of primate cognition, researchers have had great interest in whether nonhuman primates are capable of logical thinking (e.g., Premack, 1976), and conservation tasks have been used to investigate this topic (see Tomasello & Call, 1997, for a review). There have been four studies directly examining liquid conservation in nonhuman primates. Woodruff, Premack, and Kennel (1978) gave their female chimpanzee, Sarah, a series of conservation tasks involving either liquid (colored water), solid (clay), or number (buttons). Sarah had previously acquired an accurate use of plastic tokens that stand for *the same* and *different.* In a liquid conservation task, for instance, she was first presented with a pair of identical glasses filled with either equivalent or different amounts of water. One of the quantities was then poured into another glass of a different proportion, and she was asked to judge the stimuli by choosing either of the two tokens. She was capable of making correct judgments in the liquid and solid conservation tasks but not in number conservation tasks. The researchers concluded that inferential reasoning rather than mere perception accounted for her success because she failed to make an accurate judgment without seeing the original states of the quantities and the process of the transformation. Sarah also demonstrated a successful performance in distinguishing shape transformations from addition and subtraction manipulations.

With a different approach, Muncer (1983) attempted to clarify the ability to conserve liquid quantities in chimpanzees. The applied procedure involves unequal quantities instead of equivalent quantities and is called an *over-conservation task* as opposed to the standard Piagetian conservation task. The subjects were 2 chimpanzees, but only 1 of them completed all tasks. In Muncer's liquid conservation test, the chimpanzee was presented with a pair of identical standard receptacles filled with different amounts of syrup that was strongly favored by the animal. When allowed to indicate her choice by pointing, the subject readily selected the larger reward. The contents were then transferred into a new pair of containers, which consisted of another standard receptacle and a container with the same height and width but a greater depth. In some trials, the larger quantity went into the larger container, with the smaller being poured into the standard container, reversing the relation between the liquid levels of the quantities. The chimpanzee was successful at selecting the larger reward after the transformation. Muncer argued that perceptional judgment could not account for the chimpanzee's performance because the animal failed to make a correct choice without seeing the initial comparison and the transformation. The same subject also passed number conservation tasks. The over-conservation task may be a more promising procedure compared with the one by Woodruff et al. (1978) because it does not require that animals learn a use of communicative tokens. It can be applied to any animal that prefers

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the larger of two quantities of edible items. In fact, several studies have shown that chimpanzees and orangutans prefer the larger quantity when facing two unequal amounts of the same type of edible items (Call, 2000; Call & Rochat, 1996; Rumbaugh, Savage-Rumbaugh, & Hegel, 1987). Furthermore, this predisposition persisted in chimpanzees even in reversed contingency tasks in which the subjects were rewarded with an alternative that they did not select (Boysen, Berntson, Hannan, & Cacioppo, 1996; Boysen, Mukobi, & Berntson, 1999).

Following basically the same procedure as in the over-conservation task, Call and Rochat (1996) tested 4 orangutans for their understanding of liquid conservation. The subjects were presented with a pair of identical transparent containers filled with unequal amounts of juice and allowed to make a choice by pointing. The animals virtually always selected the larger quantity in their first choice. For instance, when a pair of identical clear glasses containing 60 ml and 30 ml of juice, respectively, were presented, all subjects selected the larger quantity in 24 of 24 trials. An experimenter then introduced two containers of different size and shape and transferred the contents of the original containers into the second pair in full view of the apes. Three of the 4 orangutans were capable of selecting the larger quantity of juice after the transformation. However, the apes showed no evidence of conservation when one of the presented quantities in a pair was split into identical multiple containers. The animals' strategy was either selecting a quantity with a higher liquid level or preferring a set of multiple containers over a single counterpart, neither of which produced conservation. The researchers concluded that the orangutans depended on perceptual information rather than logical necessity, thus demonstrating pseudoconservation when the perceptional cues made less contrast with the actual quantitative relation. Call and Rochat (1996) also conducted the same series of conservation tasks on human children at 6–8 years of age. In contrast with the orangutans, 2 of the 10 children were able to pass all of the tests, showing evidence of true conservation satisfying the original definition proposed by Piaget and Inhelder (1941).

Call and Rochat (1997) further investigated perceptual strategies underlying the orangutans' pseudoconservation. The subjects were 4 orangutans, 3 of which had participated in the previous experiment. The researchers proposed three possible tactics that were based on perception: a visual estimation, a use of pouring cues, and a tracking strategy. To see whether the subjects could make accurate estimates of liquid quantities, the researchers presented the orangutans with two different amounts of juice in a pair of transparent containers of different shapes. All of the subjects could successfully select the larger quantity when the shapes of the containers were more comparable. The researchers next tested whether the subjects were able to use pouring cues that were available during the transfer of liquid. Two different amounts of juice were transferred from two identical opaque cups into another pair of identical opaque cups in front of the apes, after which the animals were allowed to make their choice. The orangutans showed low accuracy in selecting the larger quantity except for 1 subject who demonstrated some evidence of the use of the pouring cues. Finally, the apes' use of tracking strategy was examined. Different quantities of juice were transferred from a pair of identical clear cups into a pair of identical opaque cups in full view of the orangutans. The positions of the opaque containers remained unchanged in half of the trials, whereas the positions were switched prior to the apes' choice in the other half. Overall, 3 of the 4 apes were capable of tracking the larger quantity after the transfer, with 1 subject performing significantly better than chance even when the locations of the opaque cups changed before his choice. The researchers concluded that among the three possible tactics, the visual estimation strategy best accounted for the orangutan's pseudoconservation.

Altogether, two of the studies concluded that chimpanzees made correct conservation judgments on the basis of logical thinking, whereas the two other studies revealed that orangutans' judgment could deteriorate substantially because of distinctive changes in the liquid's appearance. Thus, whereas the studies with chimpanzees support the notion of conservation on the basis of the identity principle, the studies with orangutans support the notion of pseudoconservation on the basis of perceptual estimation. Because both the species and methods used in both sets of studies were not comparable, one cannot know whether (a) chimpanzees and orangutans differ in the mechanisms they use to solve conservation problems or (b) the differences were a result of the methods used in each set of studies.

The purpose of this study was to resolve this discrepancy by investigating the conservation skills of chimpanzees and orangutans using the same methods. Following the previously developed over-conservation method, we compared the ability to conserve liquid quantities in chimpanzees, orangutans, and bonobos (a species not previously tested in conservation tasks). We used identical methods with the three species and examined the apes' strategies for solving a series of problems. The identical experimental procedures do not necessarily ensure that the three species perceive these tasks in the same way, because of phylogenic differences; this is a general problem in comparative psychology. However, the three species of great apes belong to the same family, and their phylogenic differences should not be major obstacles to examining their conservation skills with the identical methods. Throughout the study we assessed the interplay between perceptual estimation of liquid quantities and the principle of identity. This interplay is particularly important because some studies have shown that when 4-year-old children who fail traditional liquid conservation tasks are prevented from seeing the outcome of the liquid transformations (thus freeing them from the misleading appearance of liquid) they can revert to using the identity principle and succeed in those tasks (Bruner, 1964, 1966).

Experiment 1

The purpose of this experiment was to assess the effect of seeing liquid quantities inside containers after a transformation had taken place. We presented a pair of identical transparent cups filled with different quantities of juice to the apes, and once they had selected one of them, we poured both quantities into a set of new containers and let them choose again. The first choice was necessary to ensure that the apes were willing to select the larger quantity during testing. This motivation is a prerequisite for the current over-conservation study. Without confirming the apes' willingness to gain the larger quantity one cannot assess the animals' failure in the second choice, because this could be due to either a lack of conservation skills or a lack of motivation to obtain the larger quantity. We manipulated two features of the new pair of containers: transparency (clear vs. opaque) and shape (identical vs. different), the crossing of which generated four experimental conditions. These conditions allowed us to assess the effect of two perceptual aspects of the problem, such as the liquid visibility and its shape. We hypothesized that if the apes understood the invariance of liquid quantities and were immune to misleading perceptual information, they should perform equally well in all conditions.

Method

Subjects

Four bonobos (*Pan paniscus*), 5 chimpanzees (*Pan troglodytes*), and 5 orangutans (*Pongo pygmaeus*) housed at the Wolfgang Köhler Primate Research Center, Leipzig, Germany, served as subjects (see Table 1 for additional information). There were 5 males and 9 females, including juveniles, adolescents, and adults. All subjects were mother reared, except for the 3 male bonobos (1 adult, 2 juveniles) and the 2 female chimpanzees (both adults) who were hand reared. No subjects had received conservation testing prior to this study. All subjects lived in social groups of various sizes with access to indoor and outdoor areas. The subjects were individually tested in their indoor cages. The animals were fed three times a day on a diet of fruit, vegetables, monkey chow (Special Diet Services, Witham, Essex, England), and occasionally meat. Water was available ad libitum, and the subjects were not food deprived during the testing.

Apparatus

We used four types of containers. The *clear cup* was a transparent 320-ml cup (10 cm in height × 8 cm in top diameter). The *clear tube* was a transparent 60-ml test tube (11.5 cm in height × 3 cm in diameter). The *opaque cup* was a 275-ml blue cup (9.5 cm in height × 7.5 cm in top diameter). The *opaque tube* was identical to the clear tube except that it was covered with gray duct tape. Two circular pieces of cardboard of 8 cm and 4 cm in diameter served to cover the top of the opaque cup and tube, respectively, thus preventing the subjects from seeing the contents of those cups.

The containers were presented on a plastic tray (24 cm × 15 cm × 1 cm) that rested on a wooden board (75 cm × 32 cm × 1.5 cm) positioned in front of a Plexiglas window (73 cm × 60.5 cm × 2 cm). This window had three circular holes (6 cm in diameter and 23 cm apart from each other) on its lower part just above the wooden board so that the subjects could indicate their choices by sticking their fingers through one of the holes. The selected amount of juice was always transferred into a 220-ml opaque *drinking cup* (8.5 cm in height × 7.5 cm in top diameter) that differed from any of the testing containers in size and shape. We used this cup to prevent the possible confounding factor of subjects preferring to drink from particular testing cups regardless of the amount of juice they held. Two quantities (20 ml and 50 ml) of grape juice mixed with 50% water (a highly preferred drink for the apes) were used throughout the experiment.

Table 1
Age, Sex, Birthplace, and Rearing Histories of Subjects Included in the Study

Subject	Species	Age (years)	Sex	Rearing history
Joey	*Pan paniscus*	19	M	Hand reared
Kuno	*Pan paniscus*	5	M	Hand reared
Limbuko	*Pan paniscus*	6	M	Hand reared
Ulindi	*Pan paniscus*	8	F	Mother
Fifi	*Pan troglodytes*	8	F	Mother
Fraukje	*Pan troglodytes*	25	F	Hand reared
Jahaga	*Pan troglodytes*	8	F	Mother
Sandra	*Pan troglodytes*	8	F	Mother
Ulla	*Pan troglodytes*	24	F	Hand reared
Bimbo	*Pongo pygmaeus*	22	M	Mother
Dunja	*Pongo pygmaeus*	31	F	Unknown
Pini	*Pongo pygmaeus*	14	F	Mother
Toba	*Pongo pygmaeus*	8	F	Mother
Walter	*Pongo pygmaeus*	13	M	Mother

Note. All subjects were born in captivity. M = Male; F = Female.

Procedure

Pretest. Prior to the testing, we assessed whether the subjects were able to request the larger quantity of juice by pointing. The experimenter sat in front of each subject and placed the wooden platform in front of and 6–8 cm away from the Plexiglas window. She placed a pair of the identical plastic trays on the center of the platform and presented a pair of the clear cups filled with different quantities of juice (20 ml and 50 ml), with each of the cups placed on each of the plastic trays. She then slid the plastic trays from the center to opposite sides of the platform in such a way that the two containers came in front of the far right and left holes in the Plexiglas. Finally, the experimenter pushed the platform against the Plexiglas for the subject to choose one of the cups by sticking its fingers through one of the holes. The contents of the selected container was transferred into the drinking cup and given to the subject. We conducted 48 trials during this warm-up phase. Only those apes who spontaneously selected the larger quantity above chance were included in the testing phase.

Test. The procedure was identical to the pretest until the experimenter let the subject select one of the clear cups. After the subject had made a choice, the experimenter, instead of giving the selected contents to the subject, pulled back the platform to its original position and placed two empty containers side by side on the center of the platform. The type of containers depended on two factors: the visibility of the liquid and the shape of the containers. The visibility factor was categorized into clear or opaque, whereas the shape factor was categorized into same or different. The combination of these two factors generated the following four conditions:

Clear–same (CS). In this condition, a pair of clear cups were presented to the subjects.

Clear–different (CD). In this condition, a clear cup and a clear tube were presented to the subjects.

Opaque–same (OS). In this condition, a pair of opaque cups were presented to the subjects.

Opaque–different (OD). In this condition, an opaque cup and an opaque tube were presented to the subjects.

The experimenter then poured the contents of the original pair of cups into the second pair of containers and removed the original cups. In the OS and OD conditions, the opaque containers were covered with the cardboard lids immediately after the transfer to prevent the subject from seeing the contents. After the liquid transfer was completed, the experimenter placed the filled second containers onto the trays. She placed the platform against the Plexiglas so that the subject could make a second choice on the new containers and offered the contents of the selected container in the drinking cup (after transferring it from the selected container).

We conducted 24 testing trials for each condition per subject. For those conditions involving two containers of different shape (CD and OD), two types of trials were evenly assigned. In half of the trials, the larger quantity was transferred into the cup while the smaller was poured into the tube (LC trial). In the other half of the trials, the combination of the quantities and the shapes of the containers was reversed (LT trial). Besides the testing trials, we interspersed 24 pretest trials between the trials of the four testing conditions for the purpose of maintaining the animals' motivation to select the larger quantity in their first choice. Each subject received 12 sessions consisting of 10 trials each, for a total of 120 trials. Each session was a random mixture of 8 testing trials (2 trials per condition) and 2 pretest trials. Therefore, the first choice was reinforced in 20% of trials. The right and left positions of the quantities and containers were counterbalanced and randomized with a restriction that the larger quantity did not appear on the same position in more than 3 consecutive trials.

Results

Each species as a group during the test selected the larger of the two quantities of juice significantly above chance in the first choice before the transfer of the liquid quantities: bonobos, $M = 98\%$, $SD = 1.52$, $t(3) = 63.81$, $p < .001$; chimpanzees, $M = 93\%$, $SD = 5.57$, $t(4) = 17.47$, $p < .001$; orangutans, $M = 98\%$, $SD = 1.26$, $t(4) = 85.24$, $p < .001$. (The probability of a Type I error was maintained at .05 for all subsequent analyses.) Figure 1 presents the mean percentage of correct choices made by each of the three species as a function of the type of condition in the second choice following the transfer of the liquid quantities. The orangutans performed above chance in all conditions, $t(4) > 4.5$, $p < .05$, whereas the chimpanzees and bonobos did not exceed a chance level in the OD condition: chimpanzees, $t(4) = 1.50$, *ns*; bonobos, $t(3) = 2.78$, *ns*. The chimpanzees and bonobos performed above chance in the remaining three conditions: chimpanzees, $t(4) > 2.8$, $p < .05$; bonobos, $t(3) > 3.3$, $p < .05$. An analysis of variance (ANOVA) on the percentage of correct choices with condition and species as variables revealed a significant effect for condition, $F(3, 33) = 35.42$, $p < .001$, and species, $F(2, 11) = 9.65$, $p = .004$, but no Condition $\times$ Species interaction. A linear trend analysis indicated that the apes performed increasingly worse with increasing difficulty of the conditions (in the order of least to most difficult: CS, CD, OS, and OD), $F(1, 11) = 564.00$, $p < .001$.

As stated in the *Method* section, the four conditions were generated by manipulating two features of the containers into which the liquid quantities were transferred: visibility (whether the containers were transparent or opaque) and shape (whether the containers were identical or different). We assessed the effect of these two perceptual factors on the apes' performance in the following analyses. An ANOVA on the percentage of correct choices with container visibility (clear vs. opaque), container shape (same vs. different), and species as variables revealed a significant main effect of visibility, $F(1, 11) = 21.64$, $p = .001$; shape, $F(1, 11) = 129.87$, $p < .001$; and species, $F(2, 11) = 9.65$, $p = .004$, but no interaction effects. The subjects performed significantly better when the quantities were transferred into containers with the same shape (i.e., CS and OS) than when the quantities were transferred into containers with different shapes (i.e., CD and OD). Likewise, the subjects were more successful in those conditions in which the containers were clear (i.e., CS and CD) rather than opaque (i.e., OS and OD). Post hoc pairwise comparisons with the Bonferroni correction indicated that the effect of container shape was significant for each species ($p < .001$), whereas the effect of container visibility was significant for the bonobos ($p = .020$) and chimpanzees ($p = .003$) but not for the orangutans. Finally, post hoc pairwise comparisons with the Bonferroni correction revealed that the orangutans as a group had a higher mean percentage correct across the conditions (86%) than did the bonobos (78%) and chimpanzees (69%), although the group difference reached significance between the orangutans and chimpanzees only ($p = .003$). Consequently, we pooled the two species of the genus *Pan* in subsequent analyses.

Focusing on those conditions involving a shape transformation in the liquid appearance (i.e., CD and OD) allowed us to investigate more closely the pattern of errors. Recall that those conditions had two types of trials depending on the container that received the larger quantity. Accordingly, the larger quantity could be transferred into the cup and the smaller into the tube (LC trial) or vice versa (LT trial). To examine in which type of trials the apes were more vulnerable to committing a mistake, we compared the group's performance in one trial type with that of the other for each of the CD and OD conditions. Figure 2 presents the mean percentage of correct choices made by subjects of each of the two genera as a function of condition and trial type. A mixed ANOVA on the percentage of correct choices with trial type and visibility (i.e., condition) as within-subject variables and genus as a between-subjects variable revealed a significant main effect of trial type, $F(1, 12) = 9.62$, $p = .009$; visibility, $F(1, 12) = 29.79$, $p < .001$; genus, $F(1, 12) = 10.42$, $p = .007$; Trial Type $\times$ Genus interaction, $F(1, 12) = 17.45$, $p = .001$; Trial Type $\times$ Visibility interaction, $F(1, 12) = 6.41$, $p = .026$; and Trial Type $\times$ Visibility $\times$ Genus interaction, $F(1, 12) = 5.48$, $p = .037$.

Focusing on the genus *Pan*, we found that an ANOVA with trial type and visibility as variables indicated a significant effect of trial type, $F(1, 8) = 42.13$, $p < .001$; visibility, $F(1, 8) = 17.41$, $p = .003$; and Trial Type $\times$ Visibility interaction, $F(1, 8) = 19.81$, $p = .002$. Post hoc pairwise comparisons with the Bonferroni correction indicated that the group of *Pan* was significantly more successful in LC trials than in LT trials in both of the two conditions, although the difference was more pronounced in the OD condition ($p < .001$) than in the CD condition ($p = .018$). In LC trials, the subjects performed significantly better than would be expected by chance for both of the CD and OD conditions: CD, $t(8) = 16.01$, $p < .001$; OD, $t(8) = 22.93$, $p < .001$. In contrast, the performance

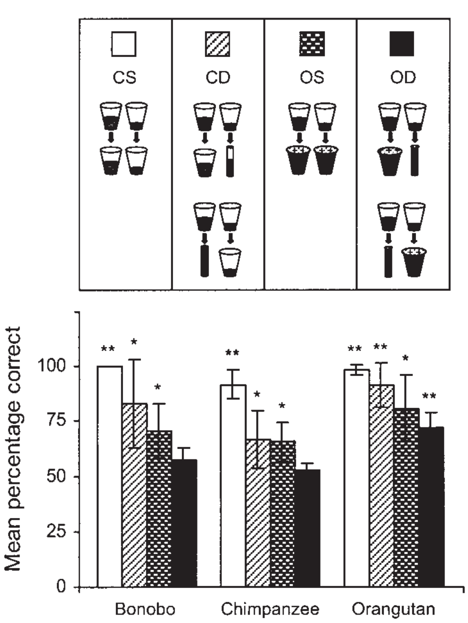

Figure 1. Mean percentage (plus or minus standard deviation) of trials in which the subjects selected the larger liquid quantity after the transformation in the clear–same (CS), clear–different (CD), opaque–same (OS), and opaque–different (OD) conditions. Liquid quantities were 20 ml and 50 ml. *$p < .05$, above chance. **$p < .01$, above chance.

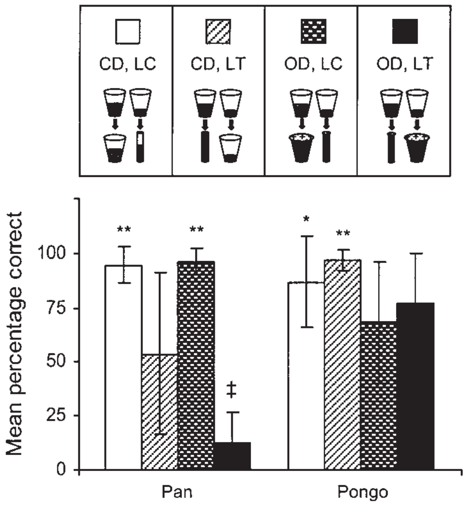

Figure 2. Mean percentage (plus or minus standard deviation) of trials in which the subjects selected the larger liquid quantity after the transformation when the larger quantity was transferred into a cup (LC) or a tube (LT) in the clear–different (CD) and opaque–different (OD) conditions. Liquid quantities were 20 ml and 50 ml. *$p < .05$, above chance. **$p < .01$, above chance. ‡$p < .01$, below chance.

in LT trials failed to differ from a chance level for the CD condition, and it was significantly below chance in the OD condition: CD, $t(8) = 0.30$, *ns*; OD, $t(8) = 8.00$, $p < .001$. Therefore, subjects of the genus *Pan* experienced more difficulty in selecting the larger quantity when the correct alternative had been transferred into the tube (LT trials) as opposed to the cup (LC trials). The poor performance in LT trials together with the high percentage of correct choices in LC trials indicated a strong preference for the cup over the tube. This preference was especially pronounced when the quantities were visually blocked from the animals.

With regard to the orangutans, we found that an ANOVA with trial type and visibility as variables indicated only the significant effect of visibility found in previous analyses, $F(1, 4) = 20.03$, $p = .011$, but no effect of trial type, $F(1, 4) = 0.36$, *ns*, and no Trial Type × Visibility interaction, $F(1, 4) = 0.01$, *ns*. In the CD condition, the orangutans performed significantly above chance in both LC and LT trials: LC, $t(4) = 3.92$, $p = .017$; LT, $t(4) = 22.96$, $p < .001$. In the OD condition, however, the orangutans' performance showed a trend of exceeding a chance level in LT trials but not in LC trials: LC, $t(4) = 1.47$, *ns*; LT, $t(4) = 2.58$, $p = .061$. Thus, the orangutans' judgment was relatively invulnerable toward the contrast between the shapes of the containers, although the group's performance deteriorated to some extent when the quantities were invisible.

Table 2 presents the performance of each subject in LC and LT trials and the likely strategies that guided their choices. In the CD condition, there were 5 subjects who followed a cup strategy (i.e., preferentially targeted the cup regardless of the amount of juice), 1 subject who followed a tube strategy (i.e., preferentially targeted the tube regardless of the amount of juice), and 1 subject whose strategy was unclear. The choices of the remaining 7 subjects were based on the contents rather than the containers, thus representing potential candidates for conservers because they were not misled by the appearance of liquid and containers. However, the results of the OD condition call this into question because no subjects

Table 2
Subjects' Performance in Two Types of Trials and Their Strategy in Experiment 1

	CD			OD		
Species and subject	LC	LT	Strategy	LC	LT	Strategy
Bonobos						
Joey	100.0**	8.3‡	Cup	100.0**	0.0‡	Cup
Kuno	100.0**	100.0**	Content	100.0**	16.7†	Cup
Limbuko	91.7**	91.7**	Content	83.3*	33.3	Cup
Ulindi	91.7**	83.3*	Content	91.7**	33.3	Cup
Chimpanzees						
Fifi	75.0	75.0	Unclear	100.0**	16.7†	Cup
Fraukje	100.0**	33.3	Cup	100.0**	0.0‡	Cup
Jahaga	91.7**	25.0	Cup	100.0**	0.0‡	Cup
Sandra	100.0**	66.7	Cup	91.7**	16.7†	Cup
Ulla	100.0**	0.0‡	Cup	100.0**	0.0‡	Cup
Orangutans						
Bimbo	91.7**	91.7**	Content	50.0	91.7**	Tube
Dunja	91.7**	100.0**	Content	66.7	83.3*	Tube
Pini	100.0**	91.7**	Content	100.0**	66.7	Cup
Toba	100.0**	100.0**	Content	91.7**	41.7	Cup
Walter	50.0	100.0**	Tube	33.3	100.0**	Tube

Note. Values are percentage of trials in which the subjects selected the larger liquid quantity after the transformation. Binomial tests were used to determine significance levels. CD = clear–different condition; OD = opaque–different condition; LC = trials in which the larger quantity was transferred into a cup; LT = trials in which the larger quantity was transferred into a tube; Cup = preferentially selecting a cup; Content = selecting the larger quantity regardless of containers; Unclear = failing to exceed a chance level in both types of trials; Tube = preferentially selecting a tube.
* $p < .05$, above chance. ** $p < .01$, above chance. † $p < .05$, below chance. ‡ $p < .01$, below chance.

showed a choice independent of the containers. Eleven subjects followed the cup strategy, whereas 3 subjects used the tube strategy, but none used the content strategy.

To examine whether there was any evidence of improvement in the course of the experiment, we analyzed the subjects' performance across 6-trial blocks (four blocks = 24 trials). An ANOVA on the percentage of correct responses with trial block and species as variables indicated no significant effect of trial block in any of the conditions: CS, $F(3, 33) = 1.56$, *ns*; CD, $F(3, 33) = 1.06$, *ns*; OS, $F(3, 33) = 1.71$, *ns*; OD, $F(3, 33) = 0.76$, *ns*. There were no interaction effects. A linear trend of increasing success across blocks would have implied a possible learning effect, but no such tendency was found across conditions: CS, $F(1, 11) = 0.38$, *ns*; CD, $F(1, 11) = 0.00$, *ns*; OS, $F(1, 11) = 4.18$, *ns*; OD, $F(1, 11) = 1.03$, *ns*. Altogether, there was no evidence of improvement across trials in any condition.

Discussion

The apes selected the larger of two quantities presented in identical clear cups (in pretest trials and in the first choice) and were generally competent after a transformation in the four testing conditions. Each of the two *Pan* species performed significantly better than a chance level in all but the OD condition, and the orangutans demonstrated an above-chance performance in all conditions. However, the apes' performance was not free from perceptual factors in judging the liquid quantities. Both container shape and liquid visibility had a significant impact on the subjects' choices.

As for container shape, we found that a transformation of the initial pair of quantities into a pair of containers with different shapes disrupted the apes' performance to some degree. More specifically, the apes' success depended on the shape of container into which the larger quantity was transferred, which suggests that the animals were somewhat vulnerable to visual changes in the appearance of the liquid or containers. This tendency was particularly pronounced in the bonobos and chimpanzees, whereas the orangutans demonstrated the trend to a lesser extent. In fact, the analyses on the type of mistakes made by subjects in the CD and OD conditions showed that the bonobos and chimpanzees, but not the orangutans, tended to avoid the tube regardless of the amount of liquid it held.

Considering liquid visibility, we found that occluding the contents of containers reduced the apes' success, which implies that the animals at least partly depended on perceptual estimation. This effect is opposite to that found in children (Bruner, 1964, 1966), because when children are prevented from seeing the end result of a transformation they improve, not decrease, their performance. These findings indicate that the apes relied on the liquid's appearance and that this information helped the apes somewhat to estimate the transformed quantities; this is unlike the findings for human children, who were simply distracted by such visual information. Also, as it was the case in the previous factor, the orangutans in general were less vulnerable to the effect of visibility than were the bonobos and chimpanzees.

Despite the influence of perceptual factors on their performance, the apes still likely possessed some intuitive appreciation of the invariance of liquid quantities. This was demonstrated by the findings that the apes had moderate success even when the quantities were transferred into opaque containers and occluded. The performance of subjects from all three species significantly exceeded a chance level in the OS condition, and the orangutans performed significantly better than would be expected by chance even in the OD condition. (The orangutans' successful performance in the latter condition is especially noteworthy because the animals had to overcome the arguably notable contrast between the different container's appearance, which the bonobos and chimpanzees failed to do.) A simple strategy of visually estimating the quantities could not account for the apes' success in these conditions. Instead, it is plausible that the apes formed mental representations of the quantities prior to the occlusion and applied these internal images to the invisible quantities. This process would require the animals to possess an appreciation of the liquid's identity.

One should note that there is an alternative interpretation other than the use of logical reasoning and visual estimation. The apes might have established a response bias toward right or left in their first choice (in which they preferentially selected the larger quantity) and persisted in the same directional response after the transfer of liquid. However, the results of Experiment 1 do not support this idea because the subjects decreased their success in their second choice compared with the first one (see Figure 1). In addition, the bonobos and chimpanzees showed this decrease in LT trials but not in LC trials (see Figure 2). Had simple repetition been responsible for their second choice, the apes should have maintained their high success rate in the second choice regardless of the conditions or trial types. Thus, the appearance of the test stimuli rather than the directional bias seemed to account for the apes' performance. Moreover, in a previous over-conservation study on orangutans, Call and Rochat (1997) found that none of their successful subjects showed such simple repetition of the preceding response. In a condition similar to the OS condition of the current experiment, their orangutans witnessed that different quantities of juice were transferred from a pair of identical clear cups into a pair of identical opaque cups. The apes made their second choice immediately after this procedure in half of the trials, whereas the locations of the opaque containers were switched prior to the second choice in the other half. Three of 4 subjects performed significantly better than chance in this condition overall, which indicates that the successful subjects did not persevere in their first directional response when the locations of the opaque containers were swapped. Taken together, in the case that visual estimation is ruled out (in the OS and OD conditions of the current experiment), an understanding of the identity principle seems to better explain the apes' successful performance than does mere repetition.

To summarize, the apes' judgment was affected by perceptual factors, although the animals might have possessed some understanding of the invariance of liquid quantities. This is especially the case for the bonobos and chimpanzees, whereas the visual information likely less affected the orangutans' performance. In the next experiment, the animals' use of visual estimation was investigated in more detail to distinguish the simple perceptual strategy from an understanding of the consistency of liquid quantities.

Experiment 2

This experiment investigated whether visual estimation alone accounted for the apes' accurate judgment of liquid quantities when the quantities remained visible after a transformation had taken place. We presented two conditions: In one condition, the subjects witnessed the transfer of two unequal amounts of juice held in two identical clear containers into two different clear containers (same as the CD condition in Experiment 1). In the other condition, the subjects had visual access only to the transformed quantities in their respective different containers without the benefit of seeing the unequal quantities before the transformation. We hypothesized that if the apes performed better in the former condition than in the latter, some strategy other than visual estimation may be at least partly responsible for the subjects' performance. In contrast, we believed that finding no difference between the conditions would indicate that the apes were merely dependent on a perceptual strategy.

Method

Subjects

The subjects were the same as in Experiment 1, except 1 chimpanzee, Sandra, who refused to participate.

Apparatus

We used the following materials from the previous experiment: clear cup, clear tube, drinking cup, juice, trays, and platform. In addition, we used a transparent circular petri dish (1.5 cm in height × 8.5 cm in diameter, with a capacity of 60 ml).

Procedure

The general procedure was identical to that of Experiment 1. The experimenter presented a pair of liquid quantities in two containers and allowed the subject to choose one of them. After the subject had chosen one of the containers, the experimenter either gave its contents to the subject or transferred the contents into another pair of containers followed by a second choice by the subject and the subsequent offer of its contents to the subject. In this experiment, we manipulated two factors: the amount of liquid in the pair of containers (same vs. different) and whether the subjects were allowed to witness the transformation (transfer vs. no transfer). The combination of these two factors generated the following four conditions:

Transfer–different (TD). The experimenter presented a pair of the identical clear cups filled with different amounts of grape juice (20 ml and 50 ml) and let the subjects select one of the containers. The first choice was necessary to confirm that the apes were motivated to select the larger quantity. After the subject's first choice, the experimenter transferred the contents of the clear cups into a pair of the dish and tube. The subject was then allowed to make a second choice and given the contents of the selected container. In half of the trials, the larger quantity was poured into the dish and the smaller quantity into the tube (LD trial), whereas in the other half the combination of the quantities and the shapes of the containers was reversed (LT trial).

No-transfer–different (NTD). The experimenter presented the two different amounts of juice (20 ml and 50 ml) directly in the pair of the dish and tube from the beginning of the trials so that the subject could see only the end result of the transformation of the quantities. After the subject's first choice, the selected quantity was immediately given to the animal. As in the previous condition, half of the trials were LD and the other half were LT trials.

Transfer–same (TS). This condition was the same as the TD condition but with equal juice quantities (50 ml).

No-transfer–same (NTS). This condition was the same as the NTD condition but with equal juice quantities (50 ml).

Overall, we conducted 24 trials for each condition per subject. As in the previous experiment, we administered 24 nontesting trials in which the different quantities were presented in a pair of the identical clear cups. The subjects immediately received the contents of the selected cup in their first choice in these trials. The nontesting trials were interspersed among the testing trials to keep the subjects motivated to select the larger quantity during testing. Each subject received six sessions consisting of 20 trials each, for a total of 120 trials. Each session was a random mixture of 16 testing trials (4 trials per condition) and 4 nontesting trials. The right and left positions of the quantities and containers were counterbalanced and randomized.

Results

As was the case in the previous experiment, all three species significantly more likely selected the larger of the two quantities when presented in identical clear cups: bonobos, $M = 96\%$, $SD = 3.54$, $t(3) = 26.17$, $p < .001$; chimpanzees, $M = 97\%$, $SD = 2.60$, $t(3) = 36.52$, $p < .001$; orangutans, $M = 98\%$, $SD = 2.53$, $t(4) = 42.33$, $p < .001$. Figure 3 shows the mean percentage of correct choices made by each of the species depending on whether the subjects witnessed the liquid transfer. The orangutans performed significantly above chance in both conditions: TD, $t(4) = 11.04$, $p < .001$; NTD, $t(4) = 7.56$, $p = .002$. Whereas the chimpanzees performed significantly above chance in the TD condition, $t(3) = 3.38$, $p = .043$, but not in the NTD condition, $t(3) = 3.08$, *ns.* The bonobos were not significantly above chance in either of the two conditions: TD, $t(3) = 1.74$, *ns*; NTD, $t(3) = 1.95$, *ns.* However, an ANOVA on the percentage of correct choices with species and the observation of the transfer (yes, no) as variables revealed no significant effect for species, $F(2, 10) = 1.52$, *ns*; transfer, $F(1, 10) = 0.91$, *ns;* or Species × Transfer interaction, $F(2, 10) = 2.58$, *ns.* If the data are collapsed across species, the apes as a group selected the larger quantity significantly more often than would be

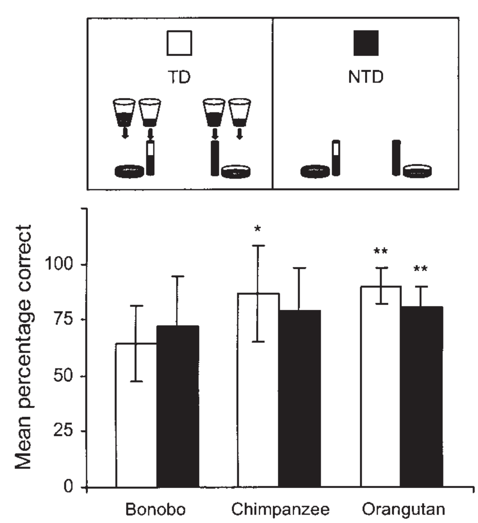

Figure 3. Mean percentage (plus or minus standard deviation) of trials in which the subjects selected the larger of unequal liquid quantities presented in a dish and a tube in the transfer–different (TD) and no-transfer–different (NTD) conditions. Liquid quantities were 20 ml and 50 ml. *$p < .05$, above chance. **$p < .01$, above chance.

expected by chance in both the TD condition, $t(12) = 6.06$, $p < .001$, and the NTD condition, $t(12) = 6.18$, $p < .001$.

We examined the possibility that the subjects improved their performance across trials by comparing the percentage of correct choices across 6-trial blocks. An ANOVA with trial block and species as variables revealed a significant effect of trial block in the TD and NTD conditions: TD, $F(3, 30) = 3.06$, $p = .043$; NTD, $F(3, 30) = 3.91$, $p = .018$. However, no significant linear trend was found in both of the conditions, which implies that the animals' performance did not gradually improve across the trial blocks: TD, $F(1, 10) = 2.64$, *ns*; NTD, $F(1, 10) = 0.00$, *ns*. Furthermore, when the performance of the first block was compared with that of the last, no significant difference was detected for both conditions: TD, $t(12) = 1.40$, *ns*; NTD, $t(12) = 1.17$, *ns*. Neither significant difference between species nor significant interaction between trial block and species was found in both conditions, suggesting that the three species did not differ from one another in terms of the sequential change in performance. Altogether, we found no evidence of learning across trials in the TD and NTD conditions.

To gain additional insight into the criteria guiding the subjects' choices in the TD and NTD conditions, we examined the percentage of correct responses in LD and LT trials. Recall that in LD trials the larger quantity was transferred into the dish, whereas in LT trials the larger quantity was transferred into the tube. Figure 4 presents the mean percentage of correct responses across species as a function of trial type (LD vs. LT) and whether the transfer was visible (TD vs. NTD). An ANOVA on the percentage of correct trials with these three variables indicated a significant effect of trial type, $F(1, 10) = 14.14$, $p = .004$, and no effect of transfer visibility, $F(1, 10) = 0.90$, *ns*; species, $F(2, 10) = 1.53$, *ns*; nor any interaction effects. The apes were significantly more successful in LD trials than in LT trials. In other words, the apes were more likely to commit an error when the larger quantity was poured into the tube as opposed to the dish.

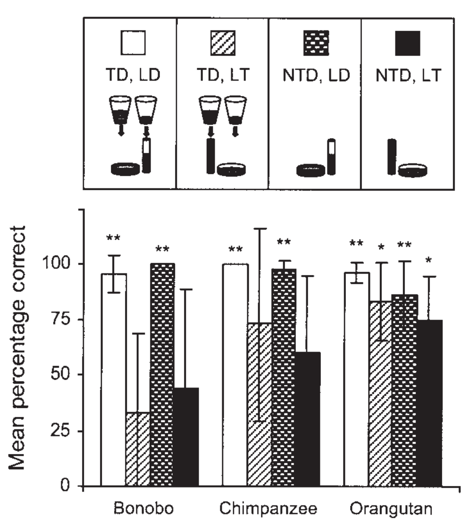

Figure 4. Mean percentage (plus or minus standard deviation) of trials in which the subjects selected the larger of unequal liquid quantities presented in a dish and a tube when the larger quantity was in a dish (LD) or a tube (LT) in the transfer–different (TD) and no-transfer–different (NTD) conditions. *$p < .05$, above chance. **$p < .01$, above chance.

In LD trials, the apes' performance as a group was significantly well above chance for both conditions: TD, $t(12) = 32.55$, $p < .001$; NTD, $t(12) = 14.56$, $p < .001$. However, the animals' performance failed to differ from a chance level in LT trials: TD, $t(12) = 1.43$, *ns*; NTD, $t(12) = 1.18$, *ns*. Although the subjects in the three great ape species were not significantly different from each other in performance, some indicative findings at the species level are worth noting here. Unlike the bonobos and chimpanzees, which yielded basically the same results as did the combined data, the orangutans as a group performed better than would be expected by chance regardless of the shape of container into which the larger quantity was poured: TD, LD, $t(4) = 22.96$, $p < .001$; TD, LT, $t(4) = 4.21$, $p = .014$; NTD, LD, $t(4) = 5.42$, $p = .006$; NTD, LT, $t(4) = 2.86$, $p = .046$ (see Figure 4). The results were consistent with the *Pongo* subjects' relative invulnerability toward arguably deceptive perceptual information, which had been also implied in Experiment 1.

Focusing on those conditions with equal liquid quantities can help to evaluate whether the subjects had a preference for the dish over the tube regardless of the amount of juice. Figure 5 presents the mean percentage of trials in which the subjects selected the dish over the tube as a function of species and whether the subjects witnessed the liquid transfer. An ANOVA on the preference score with condition and species as variables revealed no effect of condition, $F(1, 10) = 0.19$, *ns*; species, $F(2, 10) = 2.23$, *ns*; or Condition × Species interaction, $F(2, 10) = 0.05$, *ns*.

Overall, the apes' performance significantly differed from the level of 0% preference in the positive direction: TS, $t(12) = 4.41$, $p = .001$; NTS, $t(12) = 4.12$, $p = .001$. Therefore, the animals were significantly more likely to select the dish over the tube regardless of whether they had seen the transformation. This was particularly true for the bonobos and chimpanzees and to a lesser extent for the orangutans (see Figure 5). These findings seem to further support the idea that the *Pan* subjects were more easily influenced by perceptual manipulations as compared with the *Pongo* subjects.

Table 3 presents the performance of each subject in the TD and NTD conditions and the hypothesized strategies that guided their choices. In the TD condition, there were 7 subjects who followed a dish strategy, and 6 whose choices were based on the contents, independent from the shape of containers, thus representing potential candidates for conservers. Three of those 6 subjects were also able to solve the problem in the NTD condition. This means that they may have estimated the final amounts in the TD condition. However, the 3 remaining subjects developed a container strategy (1 dish and 2 tube), suggesting that they were not able to estimate the quantities. Of the 7 subjects who had shown a dish strategy in the TD trials, all but 1 subject (who was able to solve both LD and LT trials) continued to apply the dish strategy in the NTD condition.

Discussion

The results of this experiment indicate that visual estimation of quantities alone (as opposed to logical reasoning) could account for the apes' success in the CS and CD conditions of Experiment 1, in which the quantities remained visible after the transformation. When judging on the unequal amounts of juice, the apes successfully made a correct choice regardless of whether they had wit-

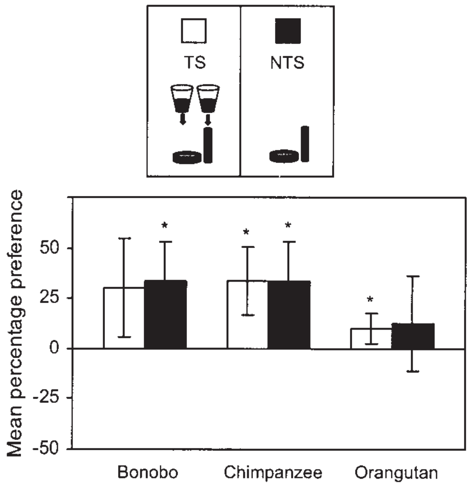

Figure 5. Mean percentage (plus or minus standard deviation) of container preference demonstrated by the subjects when the same liquid quantities were presented in a dish and a tube in the transfer–same (TS) and no-transfer–same (NTS) conditions. Positive values indicate a preference for a dish, whereas negative values indicate a preference for a tube (0% indicates that the subject had no preference). Liquid quantities were 50 ml. *$p < .05$, above chance.

nessed the transformation (in the TD condition) or not (in the NTD condition). This possible reliance on visual information is further reinforced by their bias toward the dish when equal amounts of juice were presented.

This experiment also hinted at the differences between the *Pan* subjects and the *Pongo* subjects found in the previous experiment. The bonobos and chimpanzees demonstrated a stronger preference for the contents of the dish than did the orangutans. Consequently, the accuracy of *Pan* subjects' quantitative judgment deteriorated when the larger quantity was transferred into their less favorable container (the tube) as opposed to the strongly preferred one (the dish), whereas the orangutans were successful at choosing the larger quantity no matter which container contained the larger quantity. The findings, together with those of the first experiment, support the idea that the orangutans were somewhat more resistant to the disturbance of visual stimuli. Another possible explanation is simply that bonobos and chimpanzees, unlike orangutans, had a strong impulse to avoid the specific shape of the tube, which was a pattern we also detected in Experiment 1. According to this argument, the species differences found in Experiments 1 and 2 may represent not invulnerability to deceptive visual stimuli but an avoidance of certain stimuli, such as the tube.

In Experiment 3 we tested this possibility by presenting identical containers in the transformation phase but varying their number. We transferred the original quantities into one, four, or eight identical containers. This eliminated the possibility that the subjects may have been responding to the shape of containers rather than to the visual appearance of the liquid. This next experiment also tested the apes' perceptual estimation skills by presenting a harder problem, thus making the visual estimation strategy harder to apply. We hypothesized that reducing the utility of the perceptual estimation mechanism may also enhance the use of an understanding of the liquid's identity.

Experiment 3

The previous experiments had suggested that the apes used a visual estimation strategy to select the larger of two liquid quan-

Table 3
Subjects' Performance in Two Types of Trials and Their Strategy in Experiment 2

Species and subject	TD LD	TD LT	TD Strategy	NTD LD	NTD LT	NTD Strategy
Bonobos						
Joey	100.0**	0.0‡	Dish	100.0**	0.0‡	Dish
Kuno	83.3*	50.0	Dish	100.0**	100.0**	Content
Limbuko	100.0**	75.0	Dish	100.0**	58.3	Dish
Ulindi	100.0**	8.3‡	Dish	100.0**	16.7†	Dish
Chimpanzees						
Fifi	100.0**	100.0**	Content	100.0**	91.7**	Content
Fraukje	100.0**	91.7**	Content	100.0**	83.3*	Content
Jahaga[a]	100.0**	91.7**	Content	100.0**	50.0	Dish
Ulla	100.0**	8.3‡	Dish	91.7**	16.7†	Dish
Orangutans						
Bimbo	100.0**	75.0	Dish	100.0**	50.0	Dish
Dunja[a]	91.7**	83.3*	Content	66.7	83.3*	Tube
Pini[a]	91.7**	100.0**	Content	75.0	91.7**	Tube
Toba	100.0**	100.0**	Content	100.0**	91.7**	Content
Walter	100.0**	58.3	Dish	91.7**	58.3	Dish

Note. Values are percentage of trials in which the subjects selected the larger of unequal liquid quantities presented in a dish and a tube. Binomial tests were used to determine significance levels. TD = transfer–different condition; NTD = no-transfer–different condition; LD = trials in which the larger quantity was transferred into a dish; LT = trials in which the larger quantity was transferred into a tube; Dish = preferentially selecting a dish; Content = selecting the larger quantity regardless of containers; Tube = preferentially selecting a tube.
[a] These apes are candidates for conservers.
* $p < .05$, above chance. ** $p < .01$, above chance. † $p < .05$, below chance. ‡ $p < .01$, below chance.

tities that remained visible. However, those experiments did not disprove the use of other strategies such as logical reasoning. In fact, the apes demonstrated some appreciation of the liquid's constancy in the OS and OD conditions in Experiment 1. The current experiment investigated the possibility that the animals used the concept of identity by presenting a more demanding task that made visual estimation harder. This experiment also eliminated the shape of containers as a potential confounding factor. We transferred each of two different quantities of juice from a pair of identical clear cups into a single cup and a set of multiple cups (either four or eight). Each of the cups in the multiple set received roughly equal quantities of liquid.

Method

Subjects

The subjects were the same as in Experiment 2.

Apparatus

We used the same trays, platform, and drinking cup as in Experiment 2. All containers used in this experiment were small, transparent plastic, 30-ml cups (4 cm in height × 4 cm in top diameter). We used two quantities (14 ml and 28 ml) of grape juice (nondiluted with water) throughout the experiment.

Procedure

The basic procedure was identical to that of Experiment 1 except that we used smaller quantities (14 ml and 28 ml) and one of the quantities was split into multiple containers. The experimenter presented the subject with a pair of the identical cups filled with the unequal amounts of juice in opposite sides of the platform. After the subject made a choice, the experimenter brought the trays back to the center of the platform and conducted one of the two following conditions:

4-cup. The experimenter placed a single cup and a set of four cups behind each of the original cups so that all of them were resting on the plastic trays. She transferred the contents of each original cup into the corresponding new containers. When transferring the liquid into the multiple cups, the experimenter attempted to split it into approximately equal amounts among the cups.

8-cup. This condition was the same as the 4-cup condition but with eight cups.

Once the experimenter had completed the liquid transfer, she removed the empty cups and let the subject make a second choice by sliding the trays toward opposite sides of the platform. In half of the trials, the larger quantity was poured into the single cup, and the smaller was poured into the multiple cups (LS trial), whereas in the other half, the combination of the quantities and cups was reversed (LM trial).

Overall, we conducted 24 trials for each condition per subject. In addition to the two testing conditions, we administered 12 nontesting trials (in which the subjects immediately received the designated alternative in their first choice), which were interspersed among the testing trials to maintain the subjects' motivation to select the larger quantity during the testing. Each subject received six sessions consisting of 10 trials each, for a total of 60 trials. Each session was a random mixture of 8 testing trials (4 trials per condition) and 2 nontesting trials. The right and left positions of the quantities and container sets were counterbalanced and randomized with a restriction that the larger quantity did not appear on the same position in more than 2 consecutive trials.

Results

All species selected the larger of the two quantities of juice presented in two identical cups at a rate significantly above chance: bonobos, $M = 95\%$, $SD = 2.09$, $t(3) = 42.62$, $p < .001$; chimpanzees, $M = 91\%$, $SD = 5.86$, $t(3) = 13.95$, $p = .001$; orangutans, $M = 93\%$, $SD = 5.47$, $t(4) = 17.43$, $p < .001$. Figure 6 presents the mean percentage of correct choices after the quantities were transferred into the single and the multiple cups as a function of species and condition. An ANOVA with condition and species as variables revealed a significant effect for species, $F(2, 10) = 5.62$, $p = .023$, a trend for condition, $F(1, 10) = 4.53$, $p = .059$; and a significant effect of Species × Condition interaction, $F(2, 10) = 4.37$, $p = .043$. Main effects analyses showed significant species differences in the 8-cup condition, $F(2, 10) = 7.15$, $p = .012$, and a trend of species differences in the 4-cup condition, $F(2, 10) = 3.87$, $p = .057$. Post hoc pairwise comparisons with the Bonferroni correction revealed that the orangutans as a group significantly outperformed both the bonobos ($p = .035$) and the chimpanzees ($p = .022$) in the 8-cup condition. In the 4-cup condition, the group difference reached a trend level between only the orangutans and bonobos ($p = .059$).

Because of the similarities between the bonobos and chimpanzees and their differences with the orangutans, we reanalyzed the data after pooling together the bonobos and chimpanzees. An ANOVA with condition and genus as variables revealed a significant effect for genus, $F(1, 11) = 11.69$, $p = .006$, but no effect of condition, $F(1, 11) = 1.54$, *ns*, or Genus × Condition, $F(1, 11) = 2.48$, *ns*. The orangutans significantly outperformed the bonobos and chimpanzees (and there were no differences between the 4-cup and 8-cup conditions) even though subjects of both genera were above chance in the 4-cup condition, *Pongo,* $t(4) = 7.17$, $p = .002$; *Pan,* $t(7) = 3.17$, $p = .016$, and in the 8-cup condition, *Pongo,* $t(4) = 5.07$, $p = .007$; *Pan,* $t(7) = 2.41$, $p = .047$. Nevertheless, at the species level neither bonobos nor chimpanzees reached a significant level in any of the conditions.

We investigated the pattern of errors by focusing on trial type. Recall that in LS trials the larger quantity was transferred into the single cup, whereas in LM trials the larger quantity was transferred into the multiple cups. Figure 7 presents the mean percentage of

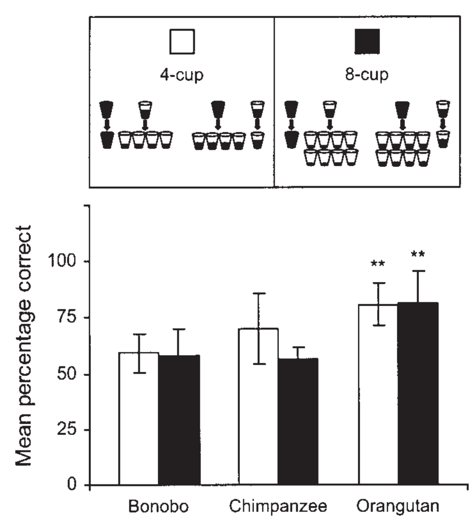

Figure 6. Mean percentage (plus or minus standard deviation) of trials in which the subjects selected the larger liquid quantity after the transformation in the 4-cup and 8-cup conditions. Liquid quantities were 14 ml and 28 ml. **$p < .01$, above chance.

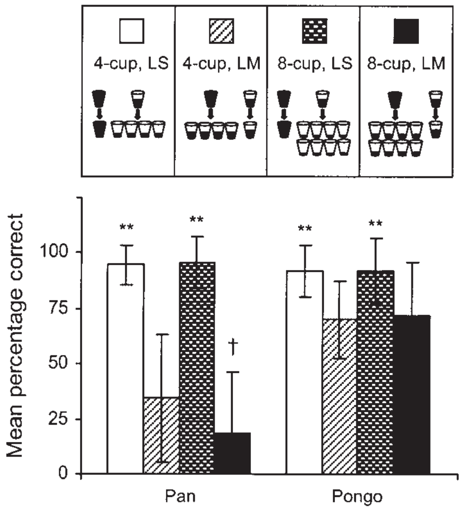

Figure 7. Mean percentage (plus or minus standard deviation) of trials in which the subjects selected the larger liquid quantity after the transformation when the larger quantity was transferred into a single cup (LS) or a set of multiple cups (LM) in the 4-cup and 8-cup conditions. Liquid quantities were 14 ml and 28 ml. ** $p < .01$, above chance. † $p < .05$, below chance.

correct choices for each genus as a function of condition and trial type. An ANOVA with genus, trial type, and condition as variables indicated a significant effect of genus, $F(1, 11) = 11.68$, $p = .006$; trial type, $F(1, 11) = 25.32$, $p < .001$; and Genus × Trial Type interaction, $F(1, 11) = 7.25$, $p = .021$. Consequently, we analyzed *Pan* and *Pongo* subjects separately.

Focusing on the genus *Pan*, we found that an ANOVA with trial type and condition as variables indicated a significant effect of trial type, $F(1, 7) = 32.31$, $p < .001$, and no effect of condition, $F(1, 7) = 3.78$, *ns*, or Trial Type × Condition interaction, $F(1, 7) = 3.62$, *ns*. The subjects were more successful in LS than LM trials regardless of the number of cups involved. The subjects performed significantly above chance in LS trials, $t(7) = 12.74$, $p < .001$. In contrast, the subjects performed significantly below chance in LM trials, $t(7) = 2.56$, $p = .037$. Therefore, the *Pan* subjects experienced greater difficulty in making a correct choice when the larger quantity was split into a set of multiple cups as opposed to when it was simply poured into a single cup.

With regard to the *Pongo* subjects, an ANOVA with trial type and condition as variables revealed no significant effect of trial type, $F(1, 4) = 3.42$, *ns*; condition, $F(1, 4) = 0.12$, *ns*; or Trial Type × Condition interaction, $F(1, 4) = 0.28$, *ns*. A comparison against chance (50%) indicated that the orangutans performed significantly above chance in LS trials, $t(4) = 7.26$, $p = .002$, but not in LM trials, $t(4) = 2.26$, *ns*. Thus, the orangutans' judgment was relatively invulnerable to the number of cups and to the final destination of the larger quantity of juice, although the group's performance deteriorated to some extent when the larger quantity was poured into the set with multiple cups.

Table 4 presents the individual performances and the likely strategies that guided the subjects' choices in LS and LM trials in the 4-cup and 8-cup conditions. In the 4-cup condition, there were 9 subjects using a single-cup strategy, 2 whose strategy was unclear, and 2 whose choices were independent from the number of cups and instead based on the contents. In the 8-cup condition, those last 2 subjects also showed a content strategy, thus repre-

Table 4
Subjects' Performance in Two Types of Trials and Their Strategy in Experiment 3

Species and subject	4-cup condition LS	4-cup condition LM	4-cup condition Strategy	8-cup condition LS	8-cup condition LM	8-cup condition Strategy
Bonobos						
Joey	100.0**	16.7†	Single	100.0**	0.0‡	Single
Kuno	100.0**	0.0‡	Single	100.0**	0.0‡	Single
Limbuko	75.0	66.7	Unclear	66.7	83.3*	Multiple
Ulindi	91.7**	25.0	Single	100.0**	16.7†	Single
Chimpanzees						
Fifi	100.0**	0.0‡	Single	100.0**	0.0‡	Single
Fraukje	100.0**	75.0	Single	100.0**	25.0	Single
Jahaga	91.7**	41.7	Single	100.0**	16.7†	Single
Ulla	100.0**	50.0	Single	100.0**	8.3‡	Single
Orangutans						
Bimbo	100.0**	75.0	Single	100.0**	75.0	Single
Dunja	100.0**	41.7	Single	100.0**	33.3	Single
Pini[a]	100.0**	83.3*	Content	100.0**	91.7**	Content
Toba[a]	83.3*	83.3*	Content	91.7**	91.7**	Content
Walter	75.0	66.7	Unclear	66.7	66.7	Unclear

Note. Values are percentage of trials in which the subjects selected the larger liquid quantity after the transformation. Binomial tests were used to determine significance levels. LS = trials in which the larger quantity was transferred into a single cup; LM = trials in which the larger quantity was transferred into a set of multiple cups; Single = preferentially selecting a single cup; Unclear = failing to exceed a chance level in both types of trials; Multiple = preferentially selecting a set of multiple cups; Content = selecting the larger quantity regardless of containers.
[a] These apes are candidates for conservers.
* $p < .05$, above chance. ** $p < .01$, above chance. † $p < .05$, below chance. ‡ $p < .01$, below chance.

senting cases of potential conservers. Of the remaining subjects, there were 9 using a single-cup strategy, 1 using a multiple-cups strategy, and 1 subject whose strategy was unclear.

To investigate whether the apes gradually learned to make a correct response, we analyzed the trials as in the previous experiments. There was no change over trials in the 4-cup condition, $F(3, 30) = 1.71$, *ns*. In contrast, there was a significant effect of trial block in the 8-cup condition, $F(3, 30) = 4.71$, $p = .008$, but the apes' performance of the first block was not significantly different from that of the last block, $t(12) = 0.64$, *ns*. In addition, no linear trend was found significant, $F(1, 10) = 0.00$, *ns*. Taken together, there was no evidence that the apes gradually learned to make a correct choice throughout testing.

Discussion

Subjects in the genus *Pan* and *Pongo* demonstrated a successful performance that significantly exceeded a chance level in both the 4-cup and 8-cup conditions, with no significant differences between the conditions. This opens the possibility that the subjects may have been using a conservation strategy. However, further analyses revealed that the division of the larger quantity reduced the accuracy of the groups' judgment, particularly for the bonobos and chimpanzees, thus replicating the greater vulnerability of *Pan* compared with *Pongo* that we detected in the previous experiments. Because the quantities were transferred into identical containers in this experiment, species differences in container preference cannot explain *Pan* subjects' greater tendency to avoid a given set of multiple cups. Overall, subjects from each of the genera successfully selected the larger quantity that was poured into the single cup but failed to do so when the larger quantity was split into multiple cups. Considering that it was arguably much more difficult to visually estimate the larger quantity in the latter type of trials than in the former, this seems to indicate that the apes relied on visual estimation and that when this possibility was prevented they resorted to nonconservation strategies such as selecting the single cup, as the individual analyses suggest. However, there were 2 orangutans (Pini and Toba) who may have followed a conservation strategy, because their choices were independent from the number of cups or the place in which the larger quantity was transferred.

To assess whether these apes were truly conserving or just able to estimate the total liquid quantities in the two sets of containers, we conducted the same manipulation as in Experiment 2. Namely, we administered trials in which the subjects were able to see the initial quantities before the transformation took place and trials in which the subjects were allowed to see the quantities only after the transformation had taken place. The outcome of this manipulation is presented in Experiment 4.

Experiment 4

This experiment investigated whether the successful performances in Experiment 3 could be explained by visual estimation alone. As in Experiment 2, the apes were allowed to see the transformation of two different amounts of juice in some conditions, whereas only the endpoint of the transformation was visually accessible to the subjects in other conditions. If the apes' performance was not different between the conditions, perceptual estimation alone could account for the animals' judgment. If the apes performed better when having witnessed the transformation, this would imply that the animals used the concept of the liquid's identity.

Method

Subjects

Subjects were 1 bonobo (Limbuko), 2 chimpanzees (Fraukje and Ulla), and 3 orangutans (Bimbo, Pini, and Toba) whose performance exceeded a chance level in either one or two of the testing conditions in Experiment 3. Although only those subjects who passed both types of trials are of interest, we included the others for comparison.

Apparatus

We used the same materials as in Experiment 3.

Procedure

We followed the same procedure as in Experiment 3 except that the transformation of the unequal liquid quantities (14 ml and 28 ml) was either visually accessible to the subjects or occluded from them, depending on conditions, in the same manner as in Experiment 2. Hence, there were four conditions. Two of these conditions, 4-cup and 8-cup conditions, were identical to those of Experiment 3. In the remaining two conditions, the subjects were allowed to see only the outcome of the transformation of the liquid quantities. In the no-transfer–4-cup condition (N4-cup), the two different quantities of juice were presented in a single cup and a set of four cups from the beginning of the trials, with one of the quantities split roughly equally into the multiple-cup set. The no-transfer–8-cup condition (N8-cup) was the same as the N4-cup condition except that eight cups were used. Thus, in both no-transfer conditions, the subjects had to make a judgment without seeing the transformation of the quantities. The subjects were given their selection immediately after their first choice.

The subjects received either two or four of the four testing conditions according to their success in Experiment 3. Thus, the 2 chimpanzees, whose success had been limited to the 4-cup condition in the previous experiment, were given only the 4-cup and N4-cup conditions in this experiment. Likewise, the bonobo subject received only the 8-cup and N8-cup conditions. Finally, the 3 orangutans received all testing conditions. In half of the trials of the testing conditions, the larger quantity was poured into the single cup with the smaller into the multiple cups (LS trial), whereas the combination was reversed in the other half (LM trial). The experimenter presented 24 trials for each condition per subject. In addition, nontesting trials (12 for *Pan* subjects and 24 for *Pongo* subjects), which were the same as those of Experiment 3, were interspersed among the testing trials. For the bonobos and chimpanzees, each subject received six sessions consisting of 10 trials each, for a total of 60 trials. Each session was a random mixture of 8 testing trials (4 trials per condition) and 2 nontesting trials. As for the orangutans, each subject received 12 sessions consisting of 10 trials each, for a total of 120 trials. Each session was a random mixture of 8 testing trials (2 trials per condition) and 2 nontesting trials. The right and left positions of the quantities and container sets were counterbalanced and randomized with a restriction that the larger quantity did not appear on the same position in more than 2 consecutive trials.

Results

All apes selected the larger of the two liquid quantities at a rate significantly above chance when the liquid was presented in two identical containers (range: 94%–100%, binomial test, $p < .001$).

Table 5 presents the percentage of correct choices across conditions for each set of cups. Four of the 5 subjects demonstrated a higher percentage of correct choices in the 4-cup condition than in the N4-cup condition, although only Toba was significantly more successful in the former condition than in the latter (Fisher test, $p = .05$). Similarly, 3 of the 4 subjects showed a greater success rate in the 8-cup condition compared with the N8-cup condition, although this difference was statistically significant only for Limbuko (Fisher test, $p = .002$).

A closer investigation of the individual strategies indicated that only Toba in the 4-cup condition and Limbuko and Pini in the 8-cup condition were likely to show conservation skills. All other subjects relied on particular strategies such as taking the single cup or being able to estimate the liquid quantity in the containers. Moreover, a group level analysis indicated that the subjects were equally successful in the transfer and no-transfer conditions, $t(5) = 1.57$, *ns*.

Discussion

Although there was some indication that the apes benefited from witnessing the transformation of the liquid when judging on the quantitative relation, it was not a robust phenomenon. Group level analyses failed to find any substantial effect, and an examination of the individual strategies showed that most subjects either used nonconservation strategies, such as picking a particular set of containers, or were good estimators of the total quantities held in each set of containers and hence did not need pretransformation information. There were 3 subjects for whom such perceptual strategies could not satisfactorily account for their improvement in those trials in which they witnessed the transformation. Because a previous study (Call & Rochat, 1997) found that orangutans do not show a directional bias (i.e., systematically selecting the same side in the first and second choices), it is conceivable that these subjects formed mental representations of liquid quantities prior to the transformation and used them to make their second choice.

Table 5
Subjects' Performance in Two Types of Trials and Their Strategy in Experiment 4

	Transfer			No transfer		
Subject	LS	LM	Strategy	LS	LM	Strategy
4-cup condition						
Pini	100.0**	75.0	Single	100.0**	66.7	Single
Toba[a]	100.0**	100.0**	Content	100.0**	58.3	Single
Fraukje	100.0**	50.0	Single	100.0**	83.3*	Content
Ulla	100.0**	33.3	Single	100.0**	0.0‡	Single
Bimbo	91.7**	100.0**	Content	91.7**	91.7**	Content
8-cup condition						
Pini[a]	100.0**	83.3*	Content	100.0**	25.0	Single
Toba	100.0**	75.0	Single	100.0**	33.3	Single
Bimbo	83.3*	91.7**	Content	100.0**	91.7**	Content
Limbuko[a]	100.0**	100.0**	Content	100.0**	25.0	Single

Note. Values are percentage of trials in which the subjects selected the larger liquid quantity after the transformation. Binomial tests were used to determine significance levels. LS = trials in which the larger quantity was transferred into a single cup; LM = trials in which the larger quantity was transferred into a set of multiple cups; Single = preferentially selecting a single cup; Content = selecting the larger quantity regardless of containers.
[a] These apes are candidates for conservers.
* $p < .05$, above chance. ** $p < .01$, above chance. ‡ $p < .01$, below chance.

General Discussion

The current study investigated whether bonobos, chimpanzees, and orangutans were able to understand that liquid quantities remain constant despite transformations of their visual appearance. Solving such a problem requires that the subjects rely solely on the concept of identity while overcoming misleading visual information. Throughout the experiments there are three lines of evidence indicating that most apes were not totally free from the influence of perceptual information, although the animals also showed considerable individual differences in this capacity.

First, the apes' ability to select the larger quantity varied substantially depending on such factors as the shape or number of containers, even though the subjects were able to choose the larger of two quantities when they were presented in two identical containers. In fact, certain kinds of transformations considerably decreased the accuracy of the apes' choices, which in some cases meant that the subjects performed below chance. For instance, the apes as a group were more successful at selecting the larger quantity when it was poured into the dish-like container as opposed to the thinner, taller container. Also, subjects in each of the genus groups performed successfully when the larger quantity was transferred into the single cup but failed to do so when it was poured into the set of multiple cups. In each of these studies we were able to identify nonconservation strategies such as selecting the single cup, the tube, or the dish regardless of the amount of liquid they contained. The findings imply that the liquid's appearance misled the apes to make an inaccurate visual estimation in certain transformations.

Second, the group analyses in Experiments 2 and 4 revealed no clear evidence that the apes benefited from witnessing the liquid's transformation, which suggests that visual estimation could be entirely responsible for the apes' performance when the quantities were visible across the transfer. Finally, occluding the visual appearance of the liquid in Experiment 1 after the transformation (in the OS and OD conditions) reduced the subjects' accuracy for selecting the larger liquid quantity. This was the opposite effect than we had expected if the liquid's appearance was responsible for only the decrease in performance. In fact, children presented with a similar situation show an improvement in performance because they do not have to fight against the arguably deceptive appearance of liquid (Bruner, 1964, 1966). However, this decreased performance would be expected if the subjects were estimating the quantities after the transformation because this information is unavailable. Thus, this unexpected result supports the idea that the apes were trying to estimate the liquid quantities after the transformation had taken place. To put in a different way, although the liquid's appearance seems to be just misleading for children, it could be helpful information for the apes, albeit not always (the liquid's appearance also misled the apes to make an inaccurate estimation in certain transformations). At the group level, therefore, it can be concluded that the apes' appreciation of the liquid's identity was overwhelmed by the intervention of visual stimuli.

Despite the fact that the results were in greater part determined by the perceptual information available, it would be erroneous to conclude that there were no other factors determining the subjects' choices. There are three reasons that suggest otherwise. First, the apes seem to have possessed some appreciation of liquid quantities' invariant nature. Each of the species as a group demonstrated an above chance performance when the quantities were transferred from the pair of clear cups into the pair of opaque cups (in the OS condition in Experiment 1). Visual estimation can be ruled out in this condition because the apes were not able to see the quantities when making a judgment. Instead, the apes formed mental representations of the quantities prior to the transfer and used this information after the occlusion of the quantities. If the apes had ignored that the liquid's properties remained unchanged, they could not have applied the acquired mental images to the invisible quantities. Hence, this representational mechanism appears to reflect some understanding of the liquid's identity.

Second, one should note that the overall scores of the apes throughout the tests were often above chance. This performance compares favorably to those of children younger than 7 years of age. Although some subjects selected the cup in all trials in Experiment 1, it is clear that not all subjects did so. If certain strategies such as choosing the single cup explained the results, the subjects would only choose correctly in half of the trials in Experiment 3, but they did not. They performed much better. Finally, there were some individual subjects whose choices cannot be solely explained by perceptual factors. For instance, several apes (Dunja, Jahaga, and Pini) were able to select the larger quantity in the dish-tube test on the basis of the content strategy only if they were allowed to see the transformation. Toba, Limbuko, and Pini were also able to successfully select the larger liquid quantity in the multiple-cups experiment but only if they were able to witness the transformation. Therefore, some individuals were competent in particular tasks, and it is possible that they applied logical reasoning in at least some specific cases. Nevertheless, even these relatively competent animals were not consistently successful across the conditions, which means that their understanding of the liquid's identity could be overwhelmed by perceptual information depending on the circumstances. For instance, none of these apes was able to overcome the perceptual information in the OD condition in Experiment 1.

With regard to mechanisms underlying the apes' response, one should also note that the apes' successful performance in the current study cannot be explained by a directional response bias. This third possible mechanism presumes that the apes acquired a directional bias in the first choice (in which they preferentially selected the larger quantity) and continued to elicit the same bias in the second choice, which automatically resulted in a successful response. However, simply persevering in the preceding directional response is not consistent with our data because the apes' success deteriorated in the second choice as compared with the first one. Taking Experiment 1 as an example, the bonobos and chimpanzees showed this decrease especially in LT trials, whereas the orangutans showed the decrease in the OD condition (see Figure 2). The apes' success in the second choice deteriorated to a different degree depending on the conditions and trial types, which indicates that perceptual information rather than the directional bias appeared to account for our current results. Moreover, in a previous over-conservation study, Call and Rochat (1997) found that their orangutans did not show the perseveration of the previous directional response in the second choice when the locations of the containers were swapped. Therefore, an appreciation of the identity principle, instead of simple repetition, seems to be responsible for the apes' successful performance in the case that visual estimation is ruled out (i.e., in the OS and OD conditions of Experiment 1 and in comparative analyses between transfer and no-transfer conditions in Experiments 2 and 4).

Besides the important individual differences observed in these series of experiments, there were also important differences between the two genera, *Pan* and *Pongo.* Although subjects of the three tested species showed the conflict between an appreciation of the liquid's identity and the reliance on visual information, the orangutans tended to outperform the bonobos and chimpanzees across the experiments, showing a higher tolerance for potentially misleading visual stimuli. This orangutan's superiority is noteworthy because previous studies seemed to indicate that chimpanzees perform better than orangutans (Call & Rochat, 1996; Muncer, 1983; Woodruff et al., 1978). The findings in the OD condition deserve special attention in this regard. The orangutans as a group, but neither the bonobos nor the chimpanzees, successfully selected the larger quantity when the quantities were transferred from the pair of identical clear cups into the opaque containers of different shape. In this condition, the orangutans based their judgment almost certainly on an appreciation of the liquid's identity because they could not visually estimate the occluded quantities. At the same time, they must have overcome the visual contrast between the opaque cup and the opaque tube. Therefore, only the orangutans gave definite indications that they could simultaneously achieve the two cognitive requirements for an understanding of liquid conservation, if not unconditionally.

Assuming that this is a genuine difference between genera, one may ask about the basis for orangutans' better management of perceptual disturbances. There are at least two possibilities. One possibility is that orangutans' sense of the liquid's identity is more firmly established than that of chimpanzees and bonobos. In other words, orangutans may have more understanding that liquid quantities are constant regardless of changes in appearance and may be able to keep better track of them. Another possibility is that edible items cause lesser interference in the judgment of orangutans than they do in chimpanzees and bonobos. This hypothesis is compatible with previous studies on reversed contingency. In this paradigm, subjects are given two unequal amounts of food and asked to make a choice. Because an experimenter always gives the subjects the unselected quantity, the subjects' optimal response is to choose the smaller quantity so that they can obtain the larger portion of food. Chimpanzees have a hard time solving this task even after hundreds of trials (Boysen & Berntson, 1995; Boysen et al., 1996, 1999; Boysen, Berntson, & Mukobi, 2001). Boysen and her colleagues concluded that the chimpanzees' predisposition to reach for the larger quantity of food has a strong interference on the animals' performance. In sharp contrast to these findings, one study reported that two orangutans were able to develop the optimal strategy of selecting the smaller amount of food in a similar reversed contingency task (Shumaker, Palkovich, Beck, Guagnano, & Morowitz, 2001). This difference between chimpanzees and orangutans may be similar to the differences found in the current study. It is conceivable that *Pan* subjects' stronger tendency toward immediate gratification overshadows their ability to engage logical thinking, namely, an appreciation of the concept of identity. As Shumaker et al. (2001) argued, contrasting social systems of the two genera might contribute their different attitudes toward food items. Competition with conspecifics over food appears to be more intense and direct in a fission–fusion society of chimpanzees, for instance, than in a relatively dispersed society of orangutans. Perhaps an impulsive response to the larger (or seemingly larger) quantity of edible items might have more evolutionary importance for chimpanzees as compared with orangutans. Nevertheless, one should remain cautious about generalizing the findings in the current study and the cited experiments because of their small sample sizes. Further studies must be conducted to explore the cognitive dissimilarities between *Pan* and *Pongo.*

In conclusion, at the group level, this study produced no robust evidence that either orangutans or chimpanzees and bonobos were capable of liquid conservation solely on the basis of logical necessity or the principle of identity. Instead, changes in visual appearance of the liquid and containers substantially affected the subjects' choices in a variety of situations. Therefore, the results of the current study are best characterized as evidence for pseudoconservation (Piaget & Inhelder, 1941), in which perceptual rather than logical aspects predominate in the solution of these problems. However, perceptual predominance should not be equated to mere perceptual interference because, contrary to our expectations, removing perceptual information about the liquid's appearance after the transformation (which could potentially interfere with the subjects' choices) invariably reduced the subjects' accuracy. This is the opposite result to that found in children younger than 7 years of age, for which perceptual interference appears to explain their failure to solve this task (Bruner, 1964, 1966). Unlike human children, the apes could take advantage somewhat of the liquid's appearance to visually estimate the liquid quantities.

Likewise, a predominance of perceptual factors does not mean that these factors alone are responsible for the apes' performance. On the contrary, there is some evidence to suggest that the subjects also make use of the logical aspects of the problem to some extent, as indicated by the appreciation of the constancy of the quantities and the successful performance of some subjects in several problems. These results cannot be reduced to the use of perceptual and directional strategies, but the data are consistent with the use of logical strategy. Therefore, we suggest that perceptual and logical aspects operate jointly in the resolution of these problems, although it is clear that the perceptual component seems to carry more weight than the logical component in this particular task. Future studies should investigate further the interplay between perceptual and logical aspects in the context of other Piagetian conservation tasks, for instance, by replacing liquid quantities by discrete quantities such as pieces of cereal.

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