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## Piagetian conservation of discrete quantities in bonobos (*Pan paniscus*), chimpanzees (*Pan troglodytes*), and orangutans (*Pongo pygmaeus*)

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**Abstract** This study investigated whether physical discreteness helps apes to understand the concept of Piagetian conservation (i.e. the invariance of quantities). Subjects were four bonobos, three chimpanzees, and five orangutans. Apes were tested on their ability to conserve discrete/continuous quantities in an over-conservation procedure in which two unequal quantities of edible rewards underwent various transformations in front of subjects. Subjects were examined to determine whether they could track the larger quantity of reward after the transformation. Comparison between the two types of conservation revealed that tests with bonobos supported the discreteness hypothesis. Bonobos, but neither chimpanzees nor orangutans, performed significantly better with discrete quantities than with continuous ones. The results suggest that at least bonobos could benefit from the discreteness of stimuli in their acquisition of conservation skills.

**Keywords** Piagetian conservation · Apes · Discreteness of stimuli

### Introduction

Primates encounter various kinds of quantity-related problems in situations such as foraging. They might have to estimate food quantities in different patches, keep mental representations of the quantities, and operate these internal images in order to increase foraging efficiency (Tomasello and Call 1997). Whether great apes can engage in such operations with quantities has been a central question for decades, and previous studies have accumulated evidence that this is in fact the case, albeit their skills might be

still somewhat limited (e.g. Beran 2001, 2004; Biro and Matsuzawa 1999; Boysen and Berntson 1989; Call 2000; Tomonaga and Matsuzawa 2002; Rumbaugh et al. 1987; see also Tomasello and Call 1997).

A prerequisite for mathematical operations in children (and logical reasoning in a broader sense) is the concept of Piagetian conservation. Conservation, in a Piagetian sense, refers to the ability to understand that essential properties of physical substances remain invariant regardless of perceptual changes [Piaget 1997 (originally published 1941); Piaget and Inhelder 1941, 1969 (originally published 1966)]. Examples of these consistent properties are number, quantity, weight, and volume. Piaget and Inhelder (1941) devised a number of tasks to examine whether children were capable of conserving quantities after a variety of perceptual transformations. Typical conservation tasks proceed as follows: children are first presented with a pair of identical objects (say, A and B), one of which is then transformed into a different shape or configuration. After this transformation, the children are asked whether the transformed object (B') still has the same property as the other object (A). For instance, in number conservation tasks, two parallel rows of equal numbers of elements are arranged in one-to-one correspondence at the beginning of trials. One row is then transformed into a different configuration (e.g. by shortening or expanding) and the subjects are asked about the equivalence of numerals between the two sets of stimuli.

The acquisition of the conservation concept requires at least two abilities: (1) to be able to understand the invariance of object identity (i.e. an object retains the same identity and thus its essential properties should remain invariant), and (2) to be able to overcome perceptual seduction that is caused by salient changes in the appearance of stimuli (Bruner 1966). The precursor of the principle of invariant object is evident from object permanence, which is the ability to recover an object that escaped from the field of perception (Piaget 1961). Conservation tasks presumably induce cognitive conflict between logical reasoning and perception, because the invariance of identity instructs the subjects to make a conservation judgment, whereas perceptual cues such as changes in row length

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lead the subjects to produce a non-conservation judgment (Cantor 1983). Upon acquiring conservation, the subjects make their implicit understanding of invariance explicit by overcoming the distraction of perceptual information, and they successfully generalize their knowledge of invariance that used to be fragile and case-dependent (Gelman 1982). The generalized understanding now becomes logical necessity (Piaget 1964) in which the subjects reason that an object's essential properties must remain unchanged after any kind of transformation.

Given that the concept of conservation is a clear reflection of logical necessity based on the principle of identity, the assessment of conservation skills seems to be the key to testing whether apes can operate quantities in a genuinely logical manner. For instance, without understanding the invariance of numerical entities as logical necessity, a chimpanzee could not mentally combine invisible quantities with precision. Despite its significance in the formation of logical thinking, a relatively small number of studies have examined apes' conservation skills, with investigated properties limited to number, liquid quantity, and solid quantity (reviewed in Suda and Call 2004). As for the conservation of liquid quantities, chimpanzees, orangutans, and bonobos have been tested in this ability. All of these liquid conservation studies except one applied an "over-conservation" procedure in which subjects had to track a larger quantity of juice/syrup (versus a smaller quantity) as it was transformed by being poured into different shaped containers (Call and Rochat 1996, 1997; Muncer 1983; Suda and Call 2004). In the remaining study, a language-trained chimpanzee, Sarah, who had acquired the use of two tokens representing "same" and "different", respectively, judged whether a pair of liquid (or solid) quantities remained equal after one of them had undergone visual transformation (Woodruff et al. 1978). Overall results of these studies suggested that apes understood to some degree the invariance of liquid quantities because perceptual strategies such as visual estimation alone could not explain their performance. There were three lines of evidence supporting this: (1) apes were moderately successful at making a conservation judgment even when quantities were transferred into opaque containers and thus visual estimation was impossible (orangutans, Call and Rochat 1997; bonobos, chimpanzees, and orangutans, Suda and Call 2004); (2) some individuals needed to see pre-transformation states of quantities in order to make a correct judgment (one chimpanzee, Muncer 1983; one bonobo, one chimpanzee, and three orangutans, Suda and Call 2004; one chimpanzee, Woodruff et al. 1978); (3) two chimpanzees were able to distinguish mere visual transformation from addition and subtraction (Muncer 1983; Woodruff et al. 1978). In contrast, it was also found that apes were not totally free from sometimes misleading perceptual information such as container shape (orangutans, Call and Rochat 1996, 1997; bonobos, chimpanzees, and orangutans, Suda and Call 2004). Suda and Call (2004), therefore, concluded that apes used both logical reasoning (i.e. an understanding of the constancy of liquid quantities) and visual information to solve conservation problems, although the perceptual as-

pect could often overshadow the logical aspect, thus leading them to make a non-conservation judgment in some cases.

One interesting aspect of Piagetian conservation is that children develop the conservation of different properties at different times. For instance, number conservation is easier than the conservation of liquid/solid quantity for young children, and the former emerges developmentally prior to the latter (Brainerd and Brainerd 1972; Elkind 1961; Gruen and Vore 1972; Samuel and Bryant 1984; Smedslund 1961). This developmental sequence raises the possibility that the discreteness of substances is a salient feature that helps children to better understand the invariance of quantities. Peisach and Hardeman (1975) proposed that the obvious discreteness of stimulus elements facilitates subjects to understand that transformation is a mere spatial rearrangement of substance components. The theory predicts that young children will be more readily able to conserve pieces of material substance that are perceptually discrete as compared to a continuous substance (such as water or clay) whose components are too small to see.

Only two studies so far have directly assessed apes' ability to conserve sets of discrete quantities (i.e. number conservation). Using basically the same method as their liquid conservation task, Woodruff et al. (1978) attempted to test whether a chimpanzee, Sarah, was able to conserve numbers. However, they could not conduct a number conservation task on the chimpanzee because she failed to make an accurate same-different judgment in pre-tests in which quantities (two rows of buttons) were compared without any transformation. In contrast, Muncer (1983) reported that his chimpanzee was successful at selecting a larger quantity after transformation when two rows of candies were used in the over-conservation setting. Although Muncer also used liquid quantities in his testing, there was no direct comparison between these different dimensions of conservation, and only one subject completed the experiments. Further systematic investigations are necessary to explore the level of understanding of number conservation in apes using more subjects and different species.

The main purpose of the current study is to test the hypothesis that the discreteness of stimuli helps subjects to understand the conservation concept in three species of great apes, bonobos, chimpanzees, and orangutans. The study investigates whether apes follow the same cognitive pattern as children, performing better with discrete quantities than with continuous quantities (i.e. liquid). The three species are also compared to see whether they differ cognitively in conservation skills.

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### Experiment 1. Discrete quantities

The purpose of this experiment was to investigate apes' ability to understand the invariance of discrete quantities. The same procedure of over-conservation was applied as in our previous liquid conservation study (Suda and Call 2004). We presented apes with a pair of identical clear cups filled with different amounts of discrete food (instead of liquid), and let the subjects select one of the

cups. This step was necessary to confirm that the apes actually preferred the larger quantity of reward, which was a prerequisite for the current over-conservation task to work. We then transferred the contents from the original containers into a new pair of containers, producing various perceptual transformations, and examined whether the apes could track the larger quantity. In some conditions, a tube-like container and a cup were paired such that the perceptual contrast between the quantities was accentuated.

We manipulated two features of the new pair of containers: transparency (clear vs. opaque) and shape (same vs. different), and generated four testing conditions. Comparison between these conditions allowed us to assess the effects of these perceptual factors on the apes' conservation skills. If the apes' performance solely depended upon logical necessity, there should be no such perceptual effects and the apes should be equally successful across the conditions.

## Methods

### Subjects

Four bonobos, three chimpanzees, and five orangutans served as subjects (see Table 1 for additional information). All the subjects were housed at the Wolfgang Köhler Primate Research Center, and had participated in our previous liquid conservation experiments (Suda and Call 2004), in which each subject had received at least 240 testing trials in total. The current experiment was conducted after the completion of this previous study. In addition to the liquid conservation experiments, the subjects had participated in various kinds of cognitive tasks such as object permanence, relative numerosness, inferential reasoning, visual perspective, discrimination learning, social learning, and problem solving. There were five males and seven females, and the subjects' age ranged from juvenile to adult. All subjects lived with their conspecifics in social groups of various sizes in indoor and outdoor compounds. During the testing, the subjects were separated from their group members and individually tested in their indoor cages. The

animals were fed 3 times a day on a diet of fruit, vegetables, monkey chow, and occasionally meat. Water was available ad libitum and the subjects were not food deprived during the testing.

### Apparatus

The apparatus were the same as in experiment 1 of Suda and Call (2004), which examined liquid conservation, except that we introduced cereals (Fruit Loops) or raisins as the reward instead of grape juice. Cereals were used for the bonobos and orangutans, while the chimpanzees received raisins as substitutes because they showed little interest in the cereals. The cereals were ring-shaped pieces whose diameter varied from 1.6 to 2.0 cm, and were colored either green, yellow, purple, or orange. The size and color of food pieces were controlled and found to be roughly equal within a testing trial for each food type.

We used the following four types of containers as test stimuli: (1) a clear cup (a transparent plastic cup, 10 cm in height, 8 cm in top diameter, and 320 ml in volume), (2) a clear tube (a transparent plastic test tube, 11.5 cm in height, 3 cm in diameter, and 60 ml in volume), (3) an opaque cup (a blue plastic cup, 9.5 cm in height, 7.5 cm in diameter, and 275 ml in volume), and (4) an opaque tube (a plastic tube identical to the clear tube but covered with grey duct tape). Unlike the clear tube and the opaque tube, the clear cup and the opaque cup did not have the same dimensions. The opaque cup and tube were covered with circular cardboard lids of 8 cm and 4 cm in diameter, respectively, immediately after they were filled with the food. The four types of testing containers were paired and presented on two plastic trays (24 cm × 15 cm × 1 cm), which were raised by a wooden board (75 cm × 32 cm × 1.5 cm) to an appropriate level for the subjects to participate in the testing. In some trials, we paired a tube and a cup in order to accentuate the perceptual contrast between the quantities (see below). The subjects were individually tested in a testing room equipped with a plexiglas window that had three circular holes (6 cm in diameter and 23 cm from each other) lined up near its bottom. The subjects faced an experimenter and apparatus through this window, and indicated their choice

**Table 1** Age, sex, birthplace, and rearing histories of subjects included in the study. All subjects were born in captivity. *M* Male, *F* female

Subject	Species	Age (years; months)	Sex	Rearing history
Joey	<i>Pan paniscus</i>	20; 1	M	Hand-reared
Kuno	<i>Pan paniscus</i>	6; 2	M	Hand-reared
Limbuko	<i>Pan paniscus</i>	7; 3	M	Hand-reared
Ulindi	<i>Pan paniscus</i>	9; 3	F	Mother
Fifi	<i>Pan troglodytes</i>	10; 0	F	Mother
Fraukje	<i>Pan troglodytes</i>	27; 1	F	Hand-reared
Jahaga	<i>Pan troglodytes</i>	10; 0	F	Mother
Bimbo	<i>Pongo pygmaeus</i>	22; 7	M	Mother
Dunja	<i>Pongo pygmaeus</i>	30; 0	F	Unknown
Pini	<i>Pongo pygmaeus</i>	14; 10	F	Mother
Toba	<i>Pongo pygmaeus</i>	9; 2	F	Mother
Walter	<i>Pongo pygmaeus</i>	14; 0	M	Mother

by inserting a finger into one of the holes. Before giving the selected food portion to the subjects, the experimenter always transferred it into an opaque “reward cup” (8.5 cm in height, 7.5 cm in top diameter, and 220 ml in volume), which differed from the other testing containers in size and shape. The experimenter then used a “reward conveyor” (an opaque PVC tube, 20.5 cm in length and 5 cm in diameter) to smoothly transfer the food from the reward cup to the subjects’ mouths.

### Procedure

The procedure of the current experiment was identical to experiment 1 of Suda and Call (2004), which examined liquid conservation. Briefly, we first assessed whether the apes preferentially selected the larger quantity of food by manual pointing in a pre-test. The experimenter presented the apes with a pair of identical clear cups filled with two and five pieces of cereal (or raisins), and allowed the subjects to select either one of the cups. The selected contents were transferred into the reward cup, and then given to the subjects through the reward conveyor. The left and right positions of the quantities were counterbalanced and randomized. We conducted ten to 24 trials, and all the subjects spontaneously pointed at the larger quantity in >80% of the trials during this warm-up phase.

Testing was conducted after the completion of the pre-test. The testing procedure was the same as the pre-test until the experimenter let the subjects select one of the clear cups. She then, instead of offering the selected food to the apes, introduced a new pair of containers, and transferred the food quantities into them in full view of the subjects. (Where the quantities were transferred into opaque containers, the experimenter immediately covered them with lids after the transfer.) The subjects were allowed to choose one of the quantities after the transfer, and the experimenter delivered the selected contents to the apes using the reward conveyor. The following conditions were generated by manipulating two features of the new pair of containers (visibility, clear vs. opaque; and shape, same vs. different).

1. Clear–Same (CS), where the quantities were transferred into a pair of clear cups.
2. Clear–Different (CD), where the quantities were transferred into a clear cup and a clear tube.
3. Opaque–Same (OS), where the quantities were transferred into a pair of opaque cups.
4. Opaque–Different (OD), where the quantities were transferred into an opaque cup and an opaque tube.

We conducted 24 trials for each condition per subject. For those conditions involving containers of different shape (CD and OD), we administered two different types of trials. In Large-Cup (LC) trials, the larger quantity was transferred into a cup and the smaller quantity was transferred into a tube, whereas in Large-Tube (LT) trials the combination of the quantities and containers was reversed. There were the same number of LC and LT trials. The testing trials were interspersed with pre-testing trials to keep the subjects

motivated to select the larger food quantity in their first choice.

Each subject was subjected to 12 sessions consisting of ten trials each, i.e. a total of 120 trials. Each session was a random mixture of eight testing trials (two trials per condition) and two pre-test trials. Therefore, the first choice was reinforced in 20% of trials (i.e. 24 pre-test trials out of the 120 trials). The right and left positions of the quantities and containers were counterbalanced and randomized with the restriction that the larger quantity did not appear in the same position in more than two consecutive trials. The probability of a Type I error was set at 0.05 for all subsequent analyses. Parametric tests were conducted on the data to examine the significance level unless stated otherwise.

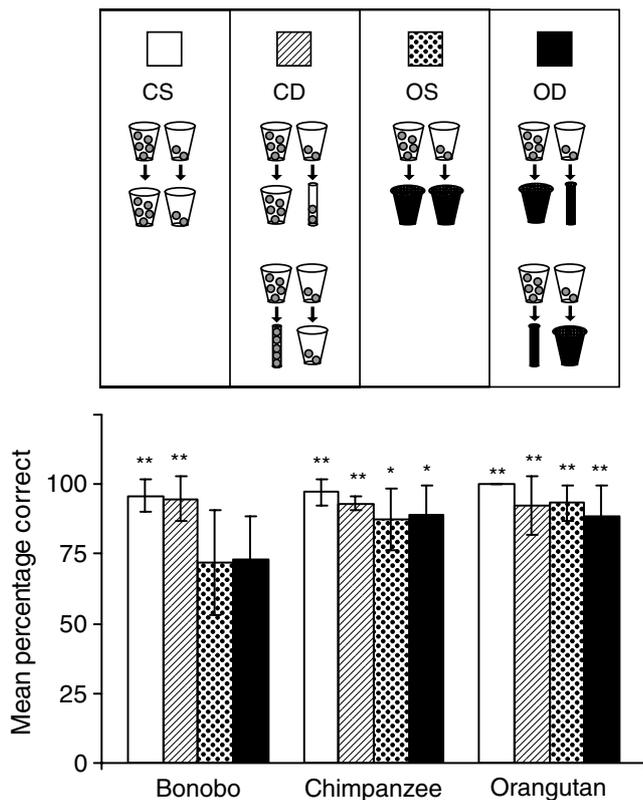
### Results

#### Overall performance

Each species as a group selected the larger of two quantities of cereals (or raisins) significantly more often than expected by chance, prior to the transfer of the food rewards: bonobos, mean ( $M$ )=97%,  $SD=3.80$ ,  $t_{(3)}=24.91$ ,  $P<0.001$ ; chimpanzees,  $M=94%$ ,  $SD=4.90$ ,  $t_{(2)}=15.52$ ,  $P=0.004$ ; orangutans,  $M=98%$ ,  $SD=2.03$ ,  $t_{(4)}=52.75$ ,  $P<0.001$ . The apes’ reliable preference for the larger quantity in their first choice held at the individual level as well. All the subjects selected the larger of two discrete quantities at a rate significantly greater than chance, prior to the transfer of the rewards (Binominal test,  $P<0.001$ ).

Figure 1 presents the mean percentage of correct choices made by each of the three species (after the transfer of food) as a function of condition. One sample  $t$ -tests were conducted on each species’ performance for each condition against the chance level of 50%. The data were corrected for multiple testing within species by using Hochberg’s improved Bonferroni method (Shaffer 1995). The orangutans as a group performed significantly above chance in all conditions,  $t_{(4)}>7.6$ ,  $P<0.01$ . Likewise, the chimpanzees successfully selected the larger quantity significantly above chance in all conditions,  $t_{(2)}>5.8$ ,  $P<0.03$ . In contrast, the bonobos’ group performance significantly exceeded a chance level only in the CS and CD conditions,  $t_{(3)}>11.3$ ,  $P<0.01$ , but not in the OS and OD conditions,  $t_{(3)}<3.0$ ,  $P>0.10$ . A mixed ANOVA on the apes’ percentage correct with condition and species as factors revealed a significant effect of condition,  $F_{(3,27)}=10.57$ ,  $P<0.001$ , with a significant Condition  $\times$  Species interaction,  $F_{(6,27)}=2.71$ ,  $P=0.034$ . Due to the significant Condition  $\times$  Species interaction, we conducted the same ANOVA on each species separately. The effect of condition was significant only for the bonobos,  $F_{(3,9)}=10.96$ ,  $P=0.002$ , whereas it was not significant for the chimpanzees,  $F_{(3,6)}=1.67$ ,  $P=0.271$ , and the orangutans,  $F_{(3,12)}=2.12$ ,  $P=0.151$ .

Table 2 presents the performance of each subject in the four testing conditions and pre-transformation data. All the



**Fig. 1** Mean percentage ( $\pm$ SD) of trials in which the subjects selected the larger discrete quantity after the transformation in the Clear-Same (CS), Clear-Different (CD), Opaque-Same (OS), and Opaque-Different (OD) conditions. Discrete quantities were two and five pieces. Data were corrected for multiple testing within species using Hochberg's improved Bonferroni method. \* $P < 0.05$ , \*\* $P < 0.01$ , above chance

chimpanzee subjects and the orangutan subjects performed significantly above chance in all conditions (Binominal test,  $P < 0.05$ ). All the bonobo subjects performed significantly above chance in the CS and CD conditions, but only one of them was significantly more successful than chance in the OS condition. In the OD condition, three of the four bonobos performed significantly better than chance, whereas the remaining subject demonstrated chance performance.

#### Reward visibility and container shape

In the current experiment, we modified two features of the containers used in the second choice: visibility (clear vs. opaque) and shape (same vs. different). To assess whether these perceptual factors had any impact on the apes' performance, a mixed ANOVA was conducted on their performance with visibility, shape, and species as factors. There was a significant effect of visibility,  $F_{(1,9)} = 22.05$ ,  $P = 0.001$ , with a significant Visibility  $\times$  Species interaction,  $F_{(2,9)} = 5.32$ ,  $P = 0.030$ , but no other effects or interactions were found. Post hoc pairwise comparisons with the Bonferroni correction showed that the apes performed better when the quantities were transferred

**Table 2** Subjects' performance in four conditions of experiment 1. Values are percentage of trials in which the subjects selected the larger of two discrete quantities after the transformation. *First choice* Subjects' choice prior to the transformation, *CS* Clear-Same condition, *CD* Clear-Different condition, *OS* Opaque-Same condition, *OD* Opaque-Different condition

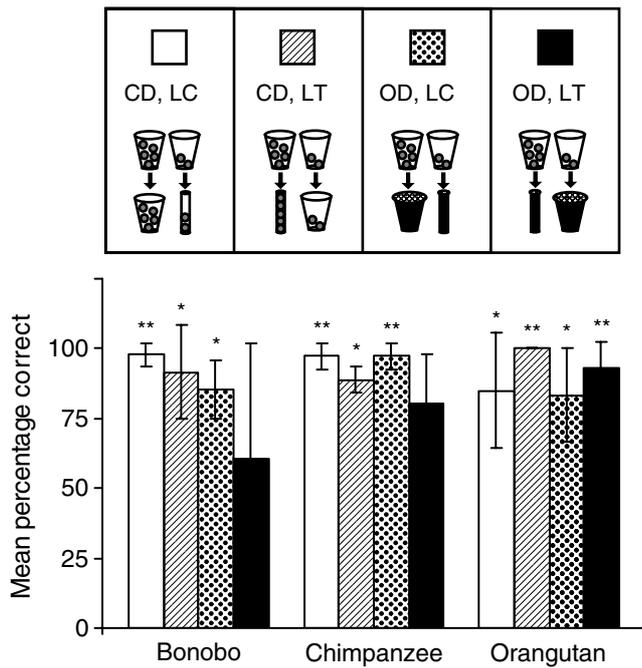
Subject	First choice	CS	CD	OS	OD
<b>Bonobos</b>					
Joey	91.7**	87.5**	83.3**	50.0	50.0
Kuno	98.3**	100.0**	100.0**	70.8	75.0*
Limbuko	100.0**	95.8**	100.0**	70.8	83.3**
Ulindi	99.2**	100.0**	95.8**	95.8**	83.3**
<b>Chimpanzees</b>					
Fifi	95.8**	100.0**	91.7**	100.0**	100.0**
Fraukje	88.3**	91.7**	91.7**	79.2**	79.2**
Jahaga	97.5**	100.0**	95.8**	83.3**	87.5**
<b>Orangutans</b>					
Bimbo	99.2**	100.0**	91.7**	95.8**	83.3**
Dunja	95.8**	100.0**	95.8**	91.7**	100.0**
Pini	99.2**	100.0**	100.0**	100.0**	75.0*
Toba	100.0**	100.0**	100.0**	95.8**	100.0**
Walter	95.8**	100.0**	75.0*	83.3**	83.3**
Trial <i>n</i>	120	24	24	24	24

\* $P < 0.05$ ; \*\* $P < 0.01$ , above chance; binominal tests were used

into clear containers (in the CS and CD conditions) than into opaque containers (in the OS and OD conditions), and this pattern was significant only for the bonobos,  $P < 0.001$  (chimpanzees,  $P = 0.190$ ; orangutans,  $P = 0.187$ ). Therefore, visibility of containers had a pronounced effect on the bonobos, but it did not significantly influence the chimpanzees and orangutans. Note also that the individual analyses revealed that some of the bonobos performed poorly in the opaque conditions, whereas all the chimpanzee subjects and the orangutan subjects performed significantly above chance in all conditions (see Table 2). In contrast, container shape did not have any significant influence on the apes' performance. The apes performed equally well irrespective of whether the quantities went into containers of different shapes or identical containers.

#### Error analysis

To further investigate the type of errors the apes committed, we focused on the different container conditions (CD and OD) and assessed the effect of trial type (LC trial vs. LT trial) on the apes' performance. In LC trials, the larger quantity was transferred into a cup, and the smaller quantity into a tube, whereas in LT trials the larger quantity was transferred into the tube and the smaller quantity into the cup. Figure 2 shows the mean percentage of correct choices made by each species after the transfer as a function of condition and trial type. An ANOVA on the percentage of correct choices with trial type, visibility (clear vs. opaque), and species as factors showed only a significant



**Fig. 2** Mean percentage ( $\pm$ SD) of trials in which the subjects selected the larger discrete quantity after the transformation when the larger quantity was transferred into a cup (*LC* Large-Cup trials) or a tube (*LT* Large-Tube trials) in the CD and OD conditions. Discrete quantities were two and five pieces. Data were corrected for multiple testing within species using Hochberg's improved Bonferroni method. \* $P < 0.05$ , \*\* $P < 0.01$ , above chance. For other abbreviations, see Fig. 1

effect of visibility,  $F_{(1, 9)} = 8.80$ ,  $P = 0.016$ . The apes were significantly more successful in the CD condition (when the quantities remained visible) than in the OD condition (when the quantities were occluded after the transfer) as found in the preceding analyses. Importantly, trial type did not have any significant effect on the apes' performance,  $F_{(1, 9)} = 0.56$ ,  $P = 0.475$ , which means that the apes as a group performed equally well regardless of whether the larger quantity was transferred into a cup or a tube. Although no significant species difference was found, the orangutans' group performance significantly exceeded a chance level in both LC and LT trials of the OD condition,  $t_{(4)} > 4.4$ ,  $P < 0.03$ , whereas each of the *Pan* species failed to perform significantly better than chance in LT trials of the OD condition: bonobos,  $t_{(3)} = 0.50$ ,  $P = 0.651$ ; chimpanzees,  $t_{(2)} = 3.05$ ,  $P = 0.093$ . (The data were corrected for multiple testing within species by using Hochberg's improved Bonferroni method.)

Although there was no significant effect of trial type at the group level, it should be noted that some subjects clearly performed better in one trial type than in the other. Out of the 12 subjects tested, two subjects (one bonobo and one orangutan) showed this pattern in the CD condition, and seven subjects (three bonobos, two chimpanzees, and two orangutans) did so in the OD condition (see Table 3). These subjects, at least partly, appeared to base their judgment on container shape, and this pattern was more pronounced when the contents were occluded.

**Table 3** Subjects' performance in two types of trials and their strategy in experiment 1. Values are percentage of trials in which the subjects selected the larger of two discrete quantities after the transformation. *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, *Tube* preferentially selecting a tube, *Content* selecting the larger quantity regardless of containers; for other abbreviations, see Table 2

Subject	CD		Strategy	OD		Strategy
	LC	LT		LC	LT	
<b>Bonobos</b>						
Joey	100.0**	66.7	Cup	100.0**	0.0(**)	Cup
Kuno	100.0**	100.0**	Content	83.3*	66.7	Cup
Limbuko	100.0**	100.0**	Content	83.3*	83.3*	Content
Ulindi	91.7**	100.0**	Content	75.0	91.7**	Tube
<b>Chimpanzees</b>						
Fifi	91.7**	91.7**	Content	100.0**	100.0**	Content
Fraukje	100.0**	83.3*	Content	91.7**	66.7	Cup
Jahaga	100.0**	91.7**	Content	100.0**	75.0	Cup
<b>Orangutans</b>						
Bimbo	83.3*	100.0**	Content	83.3*	83.3*	Content
Dunja	91.7**	100.0**	Content	100.0**	100.0**	Content
Pini	100.0**	100.0**	Content	66.7	83.3*	Tube
Toba	100.0**	100.0**	Content	100.0**	100.0**	Content
Walter	50.0	100.0**	Tube	66.7	100.0**	Tube
Trial <i>n</i>	12	12		12	12	

\* $P < 0.05$ ; \*\* $P < 0.01$ , above chance; (\*\*) $P < 0.01$ , below chance; binominal tests were used

#### Comparison with previous performance

Prior to the current experiment, all the subjects had received exactly the same testing with liquid quantities (Suda and Call 2004). To compare the apes' performance of the current experiment with that of the previous one, we conducted an ANOVA on the percentage of correct choices with experiment (current vs. previous), condition, and species as factors. (Note that the apes did not receive any new liquid trials at this point. The comparison was made between the previous experiment of liquid conservation and the current experiment of the conservation of discrete quantities.) There were significant effects of experiment,  $F_{(1, 9)} = 44.10$ ,  $P < 0.001$ , and condition,  $F_{(3, 27)} = 34.69$ ,  $P < 0.001$ , with significant interactions of Experiment  $\times$  Species,  $F_{(2, 9)} = 6.59$ ,  $P = 0.017$ , and Experiment  $\times$  Condition,  $F_{(3, 27)} = 7.98$ ,  $P = 0.001$ . Neither significant species differences nor any other interactions were found. Post hoc pairwise comparisons with the Bonferroni correction showed that the chimpanzees and orangutans were significantly more successful in the current experiment than previously: chimpanzees,  $P < 0.001$ ; orangutans,  $P = 0.017$ . The bonobos demonstrated the same pattern but the difference across the experiments was not significant,  $P = 0.075$ . Also, the apes showed an improvement in all conditions except the CS condition: CS,  $P = 0.545$ ; CD,  $P = 0.001$ ; OS,  $P = 0.045$ , OD,  $P < 0.001$ .

### Age, sex, and rearing history

Finally, we assessed the effects of three between-subject variables (i.e. age, sex, and rearing history) other than species on the performance of the apes. Because of the small sample size, we conducted an ANOVA with condition as a within-subject factor and each of these factors as a between-subject factor one at a time, instead of including all the variables at once. As for age, the subjects were divided into two groups: those who were younger than 11 years old (younger group) and those who were older than that age (older group). A mixed ANOVA with condition and age as factors revealed no significant effect of age,  $F_{(1,10)}=1.43$ ,  $P=0.260$ , or Age  $\times$  Condition interaction,  $F_{(3,30)}=0.51$ ,  $P=0.681$ . Likewise, we conducted a mixed ANOVA with condition and sex as factors on the performance of the apes. There was a significant effect of sex,  $F_{(1,10)}=6.10$ ,  $P=0.033$ , but no Sex  $\times$  Condition interaction,  $F_{(3,30)}=2.59$ ,  $P=0.071$ . Females performed significantly better than males across the four testing conditions: female,  $M=94.0\%$ ,  $SD=7.6$ ; male,  $M=83.9\%$ ,  $SD=15.3$ . With regard to rearing history, we excluded one orangutan subject (Dunja) from the analysis because the details of her rearing history were unknown. A mixed ANOVA with condition and rearing history as factors revealed a significant effect of rearing history,  $F_{(1,9)}=8.11$ ,  $P=0.019$ , and a Rearing history  $\times$  Condition interaction,  $F_{(3,27)}=8.00$ ,  $P=0.001$ . Post hoc pairwise comparisons with the Bonferroni correction indicated that mother-reared subjects performed significantly better than hand-reared subjects in the CS condition ( $P=0.011$ ) and the OS condition ( $P=0.002$ ), but not significantly better in the CD condition ( $P=0.869$ ) and the OD condition ( $P=0.059$ ). Because three of the four bonobos were males and hand-reared, it is possible that sex and rearing history might have contributed to the apparent poor performance of the bonobos.

### Discussion

Similar to our previous findings on liquid conservation (Suda and Call 2004), selecting the larger of two sets of discrete food before the quantities underwent the transformation did not pose the apes any problem. This further supports the idea that apes prefer the larger of two quantities of the same kind of food. The apes were also generally competent at tracking the larger quantity after the transformation. The chimpanzees and orangutans performed significantly above chance in all conditions. However, the bonobos as a group only reached above-chance performance in the clear conditions (CS and CD). In fact, they performed significantly better when the contents of containers remained visible after the transformation than when the rewards were occluded, which is the same pattern as that found in our previous study of liquid conservation. The poor performance of the bonobos in the opaque conditions (OS and OD), together with their competence in the clear conditions, suggests that the bonobos visually estimated the transformed quantities when possible, which

may have explained their success in the clear conditions. In contrast, container shape, which is the second perceptual factor we assessed, did not have any effect on the apes' performance at the group level. The apes were equally successful irrespective of whether containers were identical or different, and they performed equally well no matter which container (a cup or a tube) received the larger quantity, although some individuals seemed to base their judgments on container shape, at least partly.

These findings differed from our previous liquid conservation results because we had found significant effects of both visibility and container shape on the apes' performance, *Pan*'s greater vulnerability to these perceptual factors, and *Pongo*'s superior performance. Among these, only the effect of visibility was clearly detected in the current experiment for *Pan paniscus* and to a much lesser extent in *Pan troglodytes* in LT trials of the OD condition. One should be cautious also when interpreting these apparent species differences, because sex and rearing history potentially confounded the effect of species in our sample. (Note, however, no age effect was found to be significant.) We could not conclude that the discrepancies between the current and previous studies genuinely emerged from using different food stimuli (continuous or discrete food) because the current experiment was conducted after the completion of the liquid conservation experiment. The differences could be simply due to the order of task presentation and the apes' learning. We also found that the apes generally performed better in this experiment than in the previous experiment. Again, this difference could be due to the use of different food (continuous vs. discrete food) or the apes' learning.

In the next experiment, we mixed trials with continuous (i.e. liquid) and discrete quantities and examined whether any differences remained in the apes' performance between trials involving these different types of reward in an attempt to control for order effects within the experiment.

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### Experiment 2. Discrete vs. continuous quantities

This experiment investigated whether using different kinds of stimuli resulted in the previously found discrepancies between experiment 1 and our preceding liquid conservation experiment. We administered only the opaque conditions (OS and OD) because these conditions did not allow the apes to use the visual estimation strategy and thus seemed to be more demanding for the subjects. (The opaque conditions would also rule out an unwanted explanation that the relative easiness of direct visual estimation is responsible for the apes' better performance in discrete-quantity trials than in liquid ones.) If the apes continue to perform better with discrete quantities than with continuous (i.e. liquid) quantities, we can exclude the possibility of order effects and conclude that the difference is due to using different types of food. Similarly, if the effect of container shape (or trial type) is present only in the conservation of continuous quantities but not in that of discrete quantities, we should find a significant interaction of Food type  $\times$  Container shape or Food type  $\times$  Trial type.

## Methods

### Subjects

Same as in experiment 1.

### Apparatus

Same as in experiment 1 except that we did not use the clear tube.

### Procedure

The procedure was identical to that of experiment 1 and our previous liquid conservation test (experiment 1 in Suda and Call 2004). We conducted the OS and OD conditions using either continuous (i.e. liquid) or discrete quantities. In addition, we interspersed pre-test trials among the testing trials. Each subject received four sessions consisting of ten trials each, i.e. a total of 40 trials. Each session was a random mixture of eight testing trials (two trials per condition for each food type) and two pre-test trials, one of which involved continuous quantities and the other discrete quantities. The right and left positions of the quantities and containers were counterbalanced and randomized with the restriction that the larger quantity did not appear on the same position in more than two consecutive trials.

### Coding

In addition to the task performance of the apes, we coded their leaving behavior that occurred during the testing to assess their motivational states. Leaving was defined as “leaving so that the ape was out of reach of the wooden

platform, on which test stimuli rested”. The coding started when a pair of identical clear cups began to move toward the opposite sides of the platform, and ended when the subjects made their second choice.

## Results

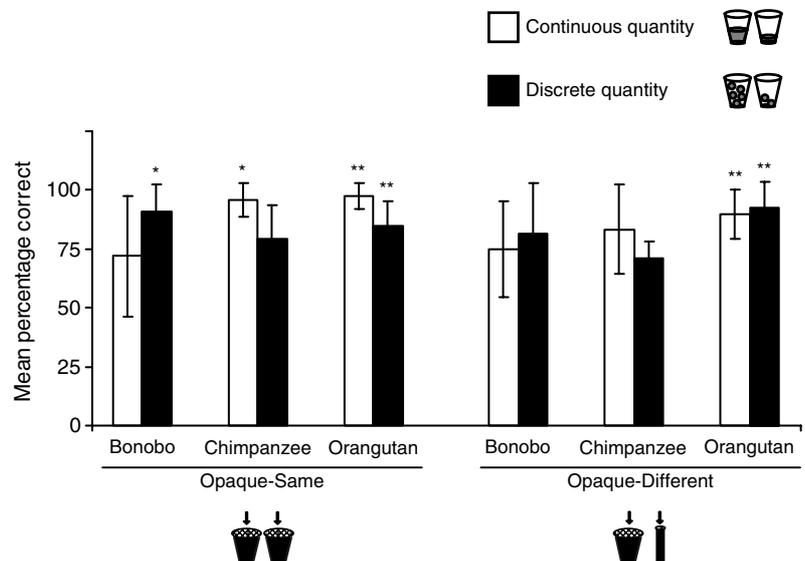
### Overall performance

Each species as a group continued to select the larger of the two unequal quantities of cereals (or raisins) when they were presented in a pair of identical clear cups for their first choice: bonobos,  $M=99\%$ ,  $SD=2.50$ ,  $t_{(3)}=39.00$ ,  $P<0.001$ ; chimpanzees,  $M=95\%$ ,  $SD=5.00$ ,  $t_{(2)}=15.59$ ,  $P=0.004$ ; orangutans,  $M=93\%$ ,  $SD=7.58$ ,  $t_{(4)}=12.68$ ,  $P<0.001$ . The inclination to select the larger quantity held at the individual level as well. All the subjects selected the larger discrete quantity at a rate significantly greater than chance, prior to the transfer (Binominal test,  $P<0.001$ ).

Similarly, each species group selected the larger of the two different quantities of juice that were presented in identical clear cups before the transfer of liquid: bonobos,  $M=99\%$ ,  $SD=2.50$ ,  $t_{(3)}=39.00$ ,  $P<0.001$ ; chimpanzees,  $M=98\%$ ,  $SD=2.89$ ,  $t_{(2)}=29.00$ ,  $P=0.001$ ; orangutans,  $M=97\%$ ,  $SD=2.74$ ,  $t_{(4)}=38.38$ ,  $P<0.001$ . Again, the preference for the larger continuous quantity was maintained at the individual level as well. All the subjects selected the larger liquid quantity at a rate significantly greater than chance, prior to the transfer (Binominal test,  $P<0.004$ ).

Figure 3 presents the mean percentage of correct choices made by each of the three species (after the transfer of food) as a function of food type and condition. A mixed ANOVA on the apes' performance with food type (discrete vs. continuous), container shape (same vs. different), and species as factors revealed a significant Food type  $\times$  Species interaction,  $F_{(2,9)}=20.96$ ,  $P<0.001$ , but no other effects or interactions (including Food type  $\times$  Container shape). Post

**Fig. 3** Mean percentage ( $\pm$ SD) of trials in which the subjects selected the larger reward quantity after the transformation in the OS and OD conditions for each type of food. Discrete quantities were two and five pieces, and continuous quantities were 20 ml and 50 ml. Data were corrected for multiple testing within species using Hochberg's improved Bonferroni method. \* $P<0.05$ , \*\* $P<0.01$ , above chance. For abbreviations, see Fig. 1



hoc pairwise comparison with the Bonferroni correction showed that the three species demonstrated different patterns of task performance across the two types of food reward (discrete vs. continuous). The bonobos were significantly more successful at selecting the larger quantity after the transfer when test stimuli were discrete quantities of food (cereals) as opposed to continuous quantities (juice),  $P=0.002$ . In contrast, the chimpanzees performed significantly better with continuous quantities than with discrete quantities,  $P=0.002$ . The orangutans did not show any significant difference in their performance between different types of food reward,  $P=0.081$ . The effect of container shape was not detected for both continuous and discrete quantities, which implies that the apes (especially the bonobos and chimpanzees) learned to overcome their container preference that had been found in our previous liquid conservation study.

Individual analyses support the different patterns of performance among species (see Table 4). Three of the four bonobos performed better with discrete rewards than with continuous rewards in the OS condition, whereas the remaining subject demonstrated a perfect performance with both types of rewards. In the OD condition, two of the four bonobos performed better with discrete quantities than with continuous ones, whereas the remaining two showed the same level of performance between the two types of rewards. All of the three chimpanzees performed better with liquid rewards than with discrete rewards in the OS condition, while two of them also showed a higher success rate with continuous quantities than with discrete ones in the OD condition.

Only the orangutans as a group performed significantly above chance in both the OS and OD conditions regard-

**Table 4** Subjects' performance in four conditions of experiment 2. Values are percentage of trials in which the subjects selected the larger of two quantities of rewards after the transformation. For abbreviations and terms, see Table 2

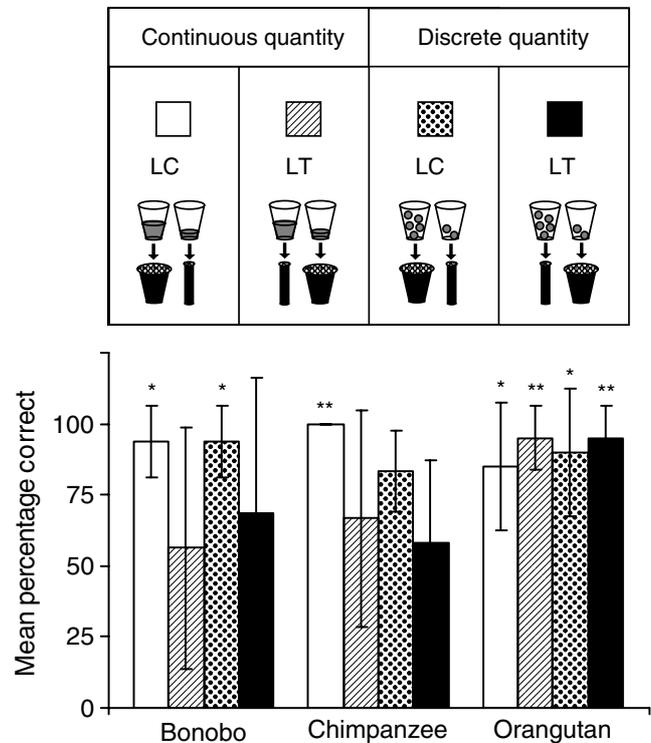
Subject	Discrete quantity			Continuous quantity		
	First choice	OS	OD	First choice	OS	OD
<b>Bonobos</b>						
Joey	100.0**	75.0	50.0	100.0**	37.5	50.0
Kuno	95.0**	87.5	87.5	95.0**	75.0	75.0
Limbuko	100.0**	100.0**	100.0**	100.0**	75.0	100.0**
Ulindi	100.0**	100.0**	87.5	100.0**	100.0**	75.0
<b>Chimpanzees</b>						
Fifi	95.0**	87.5	75.0	100.0**	100.0**	100.0**
Fraukje	90.0**	62.5	75.0	100.0**	87.5	87.5
Jahaga	100.0**	87.5	62.5	95.0**	100.0**	62.5
<b>Orangutans</b>						
Bimbo	85.0**	75.0	87.5	95.0**	100.0**	87.5
Dunja	85.0**	75.0	100.0**	100.0**	87.5	87.5
Pini	100.0**	100.0**	100.0**	95.0**	100.0**	100.0**
Toba	100.0**	87.5	100.0**	95.0**	100.0**	100.0**
Walter	95.0**	87.5	75.0	100.0**	100.0**	75.0
Trial <i>n</i>	20	8	8	20	8	8

\* $P<0.05$ ; \*\* $P<0.01$ , above chance; binominal tests were used

less of the type of food reward that was used,  $t_{(4)}>7.4$ ,  $P<0.01$ . The bonobos exceeded the chance level only in the OS condition involving discrete quantities,  $t_{(3)}=6.79$ ,  $P=0.028$ , while the chimpanzees exceeded chance only in the OS condition of continuous quantities,  $t_{(2)}=11.00$ ,  $P=0.032$ . (The data were corrected within species by using Hochberg's improved Bonferroni method.) This is consistent with our previous findings of *Pongo*'s superiority in liquid conservation.

#### Error analysis

Focusing on the OD condition and its two types of trials (LC and LT), Fig. 4 shows the mean percentage of correct choices made by each species (after the transfer) as a function of condition and trial type. To see whether the apes were more likely to commit a mistake in one trial type than in the other, we conducted a mixed ANOVA on the percentage of correct choices with trial type, food type, and species as factors. There was only a significant Food type  $\times$  Species interaction,  $F_{(2,9)}=4.97$ ,  $P=0.035$ , but no other effects or interactions were found. Post hoc pairwise comparisons with the Bonferroni correction showed that only the chimpanzees performed significantly better with continuous than with discrete food in the OD condition,



**Fig. 4** Mean percentage ( $\pm$ SD) of trials in which the subjects selected the larger reward quantity after the transformation when the larger quantity was transferred into a cup (LC) or a tube (LT) in the OD condition. Discrete quantities were two and five pieces, and continuous quantities were 20 ml and 50 ml. Data were corrected for multiple testing within species using Hochberg's improved Bonferroni method. \* $P<0.05$ , \*\* $P<0.01$ , above chance. For abbreviations, see Fig. 2

**Table 5** Subjects' performance in two types of trials and their strategy in experiment 2. Values are percentage of trials in which the subjects selected the larger of two quantities of rewards after the transformation. *Unclear* Strategy is not clear; for other strategies and abbreviations, see Table 3

Subject	Discrete quantity, OD			Continuous quantity, OD		
	LC	LT	Strategy	LC	LT	Strategy
<b>Bonobos</b>						
Joey	100.0	0.0	Cup	100.0	0.0	Cup
Kuno	75.0	100.0	Tube	75.0	75.0	Unclear
Limbuko	100.0	100.0	Content	100.0	100.0	Content
Ulindi	100.0	75.0	Cup	100.0	50.0	Cup
<b>Chimpanzees</b>						
Fifi	75.0	75.0	Unclear	100.0	100.0	Content
Fraukje	75.0	75.0	Unclear	100.0	75.0	Cup
Jahaga	100.0	25.0	Cup	100.0	25.0	Cup
<b>Orangutans</b>						
Bimbo	100.0	75.0	Cup	100.0	75.0	Cup
Dunja	100.0	100.0	Content	75.0	100.0	Tube
Pini	100.0	100.0	Content	100.0	100.0	Content
Toba	100.0	100.0	Content	100.0	100.0	Content
Walter	50.0	100.0	Tube	50.0	100.0	Tube
Trial <i>n</i>	4	4		4	4	

$P=0.026$ . The other species did not show any significant difference between continuous and discrete rewards in this condition. Importantly, trial type did not have any effect on the apes' performance in both types of conservation, meaning that the apes performed equally well regardless of whether the larger quantity was transferred into a cup or a tube. This result stands in sharp contrast with our previous results of liquid conservation. We had previously found that the bonobos and chimpanzees had a strong preference for a cup over a tube, which considerably hindered their performance in LT trials. Therefore, it is plausible that the bonobos and chimpanzees learned to select a tube when necessary.

At the individual level, however, container shape had some impact on some of the subjects. One bonobo (Joey) and one chimpanzee (Jahaga) showed a perfect performance in LC trials, but their performance was poor (no >25% correct) in LT trials (see Table 5). This indicates that they had a preference for the cup over the tube regardless of the amount of the contents. Note also that these subjects lowered the means of their groups, respectively.

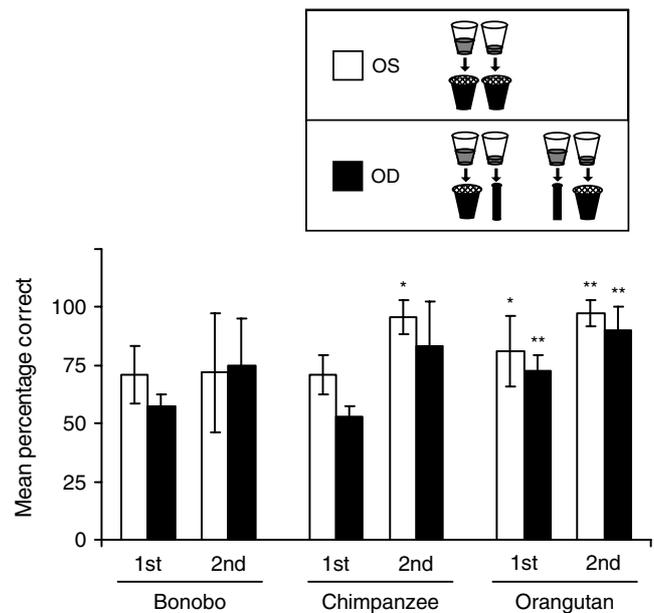
### Learning effects

Because the subjects underwent a considerable number of trials in the current study and the previous liquid conservation study, we tested whether the apes became more competent during the testing. Focusing on the OS and OD conditions in which continuous quantities were used as a reward, each subject had completed 24 trials per condition in the previous liquid conservation study, and underwent an additional eight trials per condition in the current experiment.

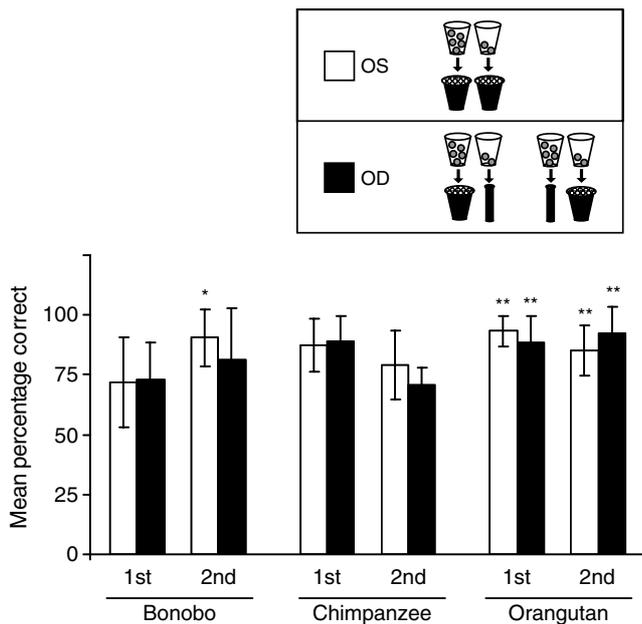
Likewise, as for the OS and OD conditions in which discrete quantities were stimuli, each subject had engaged in 24 trials per condition in experiment 1, and underwent an additional eight trials per condition in the current experiment. Comparison of the apes' performance between the first and second test phases would indicate whether there was any learning during the testing. We made this comparison for continuous and discrete food separately.

As for the conservation of continuous quantities (i.e. liquid conservation), a mixed ANOVA on the percentage of correct choices with phase (first vs. second), condition (OS vs. OD), and species as factors revealed a significant effect of phase,  $F_{(1,9)}=25.93$ ,  $P=0.001$ , and condition,  $F_{(1,9)}=7.53$ ,  $P=0.023$ , but neither significant species difference nor any interactions between the factors. The apes performed significantly better in the second phase than in the first, and were significantly more successful in the OS condition than in the OD condition. Therefore, the apes' performance improved during the testing of liquid conservation (see Fig. 5).

Concerning the conservation of discrete quantities, the same ANOVA analysis showed only a significant Order  $\times$  Species interaction,  $F_{(2,9)}=11.08$ ,  $P=0.004$ . Post hoc pairwise comparison with the Bonferroni correction revealed different patterns of sequential change across species. The bonobos were significantly more successful in the second phase than in the first, showing some evidence of learning,  $P=0.006$ . On the other hand, the chimpanzees showed an opposite pattern, performing better in the first phase than in the second, thus their success deteriorated across the phases,  $P=0.015$ . There was no significant difference



**Fig. 5** Mean percentage ( $\pm$ SD) of trials in which the subjects selected the larger continuous quantity after the transformation in the OS and OD conditions for the first and second phases of testing. Continuous quantities were 20 ml and 50 ml. Data were corrected for multiple testing within species using Hochberg's improved Bonferroni method. \* $P<0.05$ , \*\* $P<0.01$ , above chance. For abbreviations, see Fig. 1



**Fig. 6** Mean percentage ( $\pm$ SD) of trials in which the subjects selected the larger discrete quantity after the transformation in the OS and OD conditions for the first and second phases of testing. Discrete quantities were two and five pieces. Data were corrected for multiple testing within species using Hochberg's improved Bonferroni method. \* $P < 0.05$ , \*\* $P < 0.01$ , above chance. For abbreviations, see Fig. 1

in the orangutans' performance between the two phases,  $P = 0.557$  (see Fig. 6).

At the individual level, all four bonobos showed an improvement in the OS condition, and three of them did so in the OD condition as well (Tables 2, 4). In contrast, two of the three chimpanzees showed a decrease in success rate in the OS condition, and all of the chimpanzee subjects did so in the OD condition.

### Motivation

Next, we examined whether the apes showed different levels of motivation depending upon the type of rewards (i.e. discrete quantities vs. continuous quantities). Table 6 presents the percentage of trials in which each subject left the test apparatus during the testing for each of the four testing conditions (discrete quantity, OS; discrete quantity, OD; continuous quantity, OS; continuous quantity, OD). We calculated the mean of the discrete-quantity conditions and that of the continuous-quantity conditions, and conducted a Wilcoxon test with the data collapsed across species. (The nonparametric test was used because the data included many zero scores.) The apes in general left the apparatus more frequently when discrete quantities were rewards than when liquid was used instead, although this difference was not significant ( $N = 6$ ,  $T = 1.00$ ,  $P = 0.063$ ). This pattern seemed to be especially pronounced in the chimpanzees, all of which showed a higher rate of leaving in discrete-quantity trials than in continuous-quantity ones.

**Table 6** Subjects' frequency of leaving in four conditions of experiment 2. Values are percentage of trials in which the subjects left the apparatus during the testing. Mean Mean of the OS and OD conditions; for abbreviations, see Table 2

Subject	Discrete quantity			Continuous quantity		
	OS	OD	Mean	OS	OD	Mean
<b>Bonobos</b>						
Joey	0.0	12.5	6.3	12.5	0.0	6.3
Kuno	0.0	0.0	0.0	12.5	0.0	6.3
Limbuko	0.0	0.0	0.0	0.0	0.0	0.0
Ulindi	0.0	37.5	18.8	0.0	0.0	0.0
<b>Chimpanzees</b>						
Fifi	30.0	33.3	31.7	11.1	0.0	5.6
Fraukje	0.0	30.0	15.0	0.0	0.0	0.0
Jahaga	54.6	66.7	60.6	12.5	0.0	6.3
<b>Orangutans</b>						
Bimbo	0.0	0.0	0.0	0.0	0.0	0.0
Dunja	0.0	0.0	0.0	0.0	0.0	0.0
Pini	0.0	0.0	0.0	0.0	0.0	0.0
Toba	0.0	0.0	0.0	0.0	0.0	0.0
Walter	60.0	0.0	30.0	12.5	11.1	11.8

### Age, sex, and rearing history

Finally, we assessed the possible effects of three factors other than species (i.e. age, sex, and rearing history) on the performance of the apes. Due to the small sample size, we included each of these between-subject factors one at a time in an ANOVA with food type (discrete vs. continuous) and container shape (same vs. different) as within-subject factors. Neither age, sex, nor rearing history had a significant effect on the performance of the apes: age,  $F_{(1,10)} = 0.91$ ,  $P = 0.362$ ; sex,  $F_{(1,10)} = 1.61$ ,  $P = 0.233$ ; rearing history,  $F_{(1,9)} = 3.32$ ,  $P = 0.102$ . There was no significant interaction, either. Therefore, neither age, sex, nor rearing history can be responsible for the different behavioral patterns between the three species which were found in experiment 2.

### Discussion

Overall, the apes did not show a superior performance with discrete quantities than with continuous quantities. Instead, each species behaved in a different way: The bonobos performed significantly better with discrete quantities than with continuous ones, whereas the chimpanzees showed the opposite pattern. The orangutans, in contrast, were equally successful regardless of reward type.

When compared with a chance level, the orangutans succeeded in tasks regardless of conditions and type of rewards. In contrast, the bonobos performed significantly above chance only when discrete quantities were transferred into a pair of identical opaque cups, whereas the chimpanzees were successful only when continuous quantities were transferred into a pair of identical opaque cups. Neither the bonobos nor the chimpanzees succeeded in the OD condition of either reward type.

Because the apes had received more trials with continuous quantities than with discrete ones, the bonobos' better performance with discrete quantities cannot be attributed to additional experiences with discrete rewards. In addition, the bonobos were not more motivated by discrete rewards than by continuous ones. Therefore, the bonobos seemed to genuinely perform better with discrete quantities. We cannot rule out the recency effect (i.e. subjects may perform better in trials that they received more recently as compared to ones that they had experienced earlier), but the performance of the chimpanzees and orangutans seems to contradict this interpretation.

The results of the chimpanzees and orangutans are harder to interpret. The chimpanzees' superior performance with continuous quantities could have been a result of the greater number of continuous-quantity trials that they had received. Additionally, the chimpanzees were more motivated by continuous rewards than by discrete ones. The orangutans performed equally well with both types of rewards, and they seemed roughly equally motivated by both types of rewards. However, receiving a greater number of continuous-quantity trials may have eliminated the initial advantages that discrete quantities might have had.

Container shape and trial type did not have any significant effect on the apes' performance regardless of whether we used continuous or discrete quantities as a reward. Considering that container shape had influenced the apes' performance in our previous liquid conservation study, with the bonobos and chimpanzees having a relatively strong container preference for a cup, it is plausible that the apes learned to ignore container shape when making a judgment. Especially, the two *Pan* species appeared to learn to select a previously less favored tube container when it held the larger quantity.

There are two possible reasons for the apes' improved performance in liquid conservation. The first possibility is that the apes improved their performance as they underwent more trials with continuous quantities. The second supports our hypothesis: the introduction of discrete quantities facilitated the apes' understanding of invariance in general. Recall that the animals first received a series of liquid conservation experiments (in our previous study), then a discrete quantity experiment (in experiment 1), and finally a mixture of discrete and continuous-quantity trials (in experiment 2). It is possible that the discreteness of quantities helped the apes to capture the invariance of quantities in experiment 1, and they transferred this knowledge to continuous quantities. Silberberg and Fujita (1996) observed a similar performance shift in a reversed contingency task (in which the correct response was to select the smaller of two quantities of food counter-intuitively) after they made this critical principle more apparent by increasing the cost of choosing a larger reward. We did not find any learning effect in our previous liquid conservation study (Suda and Call 2004), which might favor the idea that the discreteness of quantities triggered the acquisition of the invariance principle in the apes. Yet, we cannot tease apart these two possibilities in the current study.

To sum up, only the bonobos showed some evidence supporting the idea that discrete stimuli helps subjects to understand the consistency of quantities. Container shape (or trial type) did not affect the apes' performance regardless of food type, which suggests that the apes (especially the bonobos and chimpanzees) learned to discard their container preference when making a choice.

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## General discussion

The current study tested the hypothesis that discreteness helps subjects to grasp the invariance of quantities in a Piagetian conservation task. This hypothesis is based on the findings that children perform better in conservation tasks involving discrete quantities (e.g. tokens), as opposed to continuous quantities (e.g. liquid). There was clear evidence supporting the discreteness hypothesis only for the bonobos, not for the chimpanzees or orangutans. The bonobos performed significantly better when judging discrete quantities than continuous quantities, and this difference could not be easily explained by their previous experiences. The bonobos did not show initial proficiency at selecting the larger discrete quantity in the opaque conditions (in experiment 1), which indicates that they probably did not possess the conservation concept of discrete quantities at the beginning of the current study. The fact remains, however, that the conservation task was easier for the bonobos when discrete quantities, rather than continuous ones, were used as stimuli in experiment 2. Taking a parsimonious stance, it seems that the discreteness of substances facilitated the bonobos' learning of conservation skills.

If the bonobos' behavioral pattern reflects their genuine abilities in the conservation of continuous and discrete quantities (although our sample size is too small to draw a concrete conclusion), one might ask why the discreteness of stimuli helped the subjects to grasp the constancy of quantities. One possibility is that the bonobos perceptually estimated numerical entities with accuracy (i.e. subitizing) prior to the transfer, which contributed to the formation of stable mental representations of the quantities. The numbers (2 and 5) used in this study fell within a range of subitizing (Davis and Pérusse 1988), whereas continuous (i.e. liquid) quantities did not permit the subjects such accurate estimation. It is possible that the "fiveness" of discrete food is more salient than the impression of 50 ml juice. Second, the transformation of discrete quantities might have been more observable than that of liquid quantities for our bonobos in their captive environment. There seemed to be abundant opportunities for the bonobos to manipulate discrete objects (e.g. fruits and tools) and observe the results of the manipulation. For instance, the bonobos might have changed the configuration of discrete pieces of food and observed the effect of the transformation on a daily basis. In contrast, liquid may not have been as easy to manipulate as discrete quantities because fluid required appropriate containers to be held for manipulation.

Given that object manipulation and the subsequent observation of the resulting transformation presumably play a central role in the acquisition of conservation concept (Piaget 1961), it is possible that the bonobos' daily experiences with objects was responsible for the discrepancy in the understanding of the two types of conservation. Somewhat related to this issue, the transformation of discrete quantities might be also less radical than that of continuous quantities such as liquid, because elements of discrete quantities are visible across transformation but those of liquid are not (Peisach and Hardeman 1975). Another possibility is that apes in general are attuned to dealing with discrete food rather than liquid (R. W. Wrangham, personal communication, November 2002). Food usually occurs in discrete forms (e.g. fruits) and rarely as continuous quantities. Thus, the estimation of discrete entities might be evolutionarily more significant than that of continuous quantities.

The absence of positive evidence in the other two species does not necessarily lead us to refute the hypothesis. It is possible that our experimental setting failed to probe it adequately in these species. The chimpanzees showed the opposite pattern to the bonobos by being more successful in liquid conservation, but this difference seems to reflect their fluctuating motivational states or the effect of being subject to more continuous-quantity trials, rather than different levels of cognitive competence. They were apparently less keen to obtain raisins as compared to juice, which might have become an obstacle to revealing their true cognitive skills in the conservation of discrete quantities. In fact, the chimpanzees left the apparatus more frequently in discrete-quantity trials than in continuous-quantity ones in experiment 2, and their performance deteriorated throughout the testing. The orangutans did not show any significant differences in performance between continuous and discrete quantities, with their performance nearing perfection in both types of conservation. This near ceiling level of performance may have occluded any possible discrepancies between these different types of conservation. (We did not administer more demanding tasks for the orangutans because we intended the task to be comparable across all species.) Also, being subject to more continuous-quantity trials might have compensated for the relative difficulty of the conservation of continuous quantities.

Species also differed in their overall proficiency in the task. The chimpanzees and orangutans succeeded in all conditions of experiment 1 that involved discrete quantities. In contrast, the bonobos failed in those conditions with opaque containers. One possible explanation is that the bonobos relied on the visual estimation of the post-transformation stimuli (rather than logical necessity). Even after they recovered from this failure in experiment 2, they still failed in those conditions that involved different opaque containers. The chimpanzees also experienced difficulty with different shaped containers in experiment 2, whereas the orangutans performed well in all conditions regardless the type of reward. This confirms our previous study that also showed superior performance of orangutans (Suda and Call 2004).

One should cautiously interpret these differences due to the small sample size and possible confounding factors. In fact, both sex and rearing history had a significant effect on the apes' performance in experiment 1, which means that the poor performance of the bonobos could result from the fact that three of the four bonobos were hand-reared and male. (Note, however, that age did not have any significant effect on performance in our samples.) Still, assuming that these species actually differ in conservation skills, we can speculate about the potential socio-ecological determinants of their performance. The discrepancy between *Pan* and *Pongo* in conservation skills may be explained by differences in the composition of social groups between the two genera. Orangutans are relatively solitary as compared to African apes, which live in large social groups (Kaplan and Rogers 2000). Therefore, food competition with conspecifics may be more intense in *Pan* than in *Pongo*, which might result in a greater inclination of *Pan* to reach for an apparently larger amount of food (Shumaker et al. 2001; Suda and Call 2004). Another possibility is that orangutans are better at forming mental representations of quantities and keeping them in record as compared to *Pan* species, and chimpanzees are superior to bonobos in this ability. That is to say, the differences in conservation skills among species might reflect differences in memory abilities (Suda and Call 2004). To our knowledge, no direct comparison assessing this question has been made, and it is necessary that this hypothesis be tested in future studies.

With regard to cognitive dissimilarities between the two *Pan* species, Savage-Rumbaugh and her colleagues reported that their bonobos greatly outperform chimpanzee subjects in language-related tasks, which is the opposite pattern to that which we found in the current study (Brakke and Savage-Rumbaugh 1995, 1996; Savage-Rumbaugh et al. 1985). The two species may have different cognitive advantages that are adjusted to their natural foraging ecology and communicative system. Chimpanzees may more readily solve physical cognition tasks (including the current conservation task) because protein-rich food (e.g. termites, ants, and nuts) is difficult to extract in their natural habitat and this poses challenging problems such as tracking hidden prey and using tools. On the contrary, bonobos may confront such problems less frequently because they have alternative sources of protein (e.g. protein-rich terrestrial herbaceous vegetation), which are abundant and easy to access (Malenky and Wrangham 1994). Likewise, bonobos may more readily master language skills because their natural vocalization system is more elaborate than that of chimpanzees (Bermejo and Omedes 1999). In any case, comparative studies among great ape species were neglected until recently, and more data should be collected before drawing any definite conclusions on species' differences in ape cognition.

The current study also explored the apes' competence in the conservation of discrete quantities by examining whether perceptual factors (i.e. visibility of containers and container shape) influenced task performance. We had previously found that both of these perceptual factors

had significant effects on the apes' performance in liquid conservation, with the bonobos and chimpanzees showing an especially strong container preference. In contrast, only visibility influenced the apes' performance (especially the bonobos') in the current study of discrete quantities, whereas container shape did not. The apes performed better when the quantities remained visible than when the quantities were occluded after the transformation, but they performed equally well regardless of whether containers were identical or different. Whether this discrepancy resulted from the apes' learning or the discreteness of food is inconclusive, because we found that the effect of container shape no longer existed in liquid conservation in experiment 2. Hence, the apes (more specifically *Pan* species) likely learned to overcome their container bias in our testing conditions either by receiving more trials or by taking advantage of the help of discrete quantities.

Concerning the mechanisms of the conservation of discrete quantities, two strategies were found to be underlying the apes' performance. The first tactic was visual estimation in which the apes visually estimated discrete quantities after the quantities underwent transformation. The use of visual estimation is especially evident from the performance of the bonobos. They performed significantly better when the contents of the containers were visible than when the rewards were hidden after the transformation. In fact, our subjects (all three species) seemed to be skillful at visually estimating physical quantities. We had previously found that the apes could reliably select the larger of two juice quantities that were presented in transparent containers of different shape (i.e. a dish and a tube) at the onset of trials (Suda and Call 2004). Furthermore, the apes' performance did not statistically improve when the quantities were transferred from a pair of identical clear cups into these containers of contrasting shape in full view of the apes. Therefore, it is plausible that the visual estimation strategy is sufficient for explaining the apes' successful performance in an over-conservation task (including the current study), as long as quantities are visible when the apes make a choice.

However, this perceptual strategy alone could not explain the apes' success in the opaque conditions. These conditions require mental operations beyond perception because the apes were not able to see the contents when making a final judgment in these conditions. Their judgment must have depended upon mental representations (or perceptual memory) of the earlier setting of the test stimuli. As we have argued elsewhere (Suda and Call 2004), success in these conditions appears to require subjects to form mental representations of the quantities prior to the transformation and apply this information to the occluded quantities after perceptual changes (see also Call 2000; Beran 2001). Hence, this second strategy seems to reflect the subjects' ability to understand that quantities remain constant unless any numerical operations (e.g. addition and subtraction) are conducted. It should be also noted that the chimpanzees and orangutans were successful at overcoming a salient contrast between the cup and tube in the OD condition to make a

correct judgment. This capacity of disregarding irrelevant dimensions of test stimuli is another crucial component of the conservation concept (Bruner 1966; Suda and Call 2004).

Besides the above account, there is an alternative mechanism that might have underlain the apes' performance in the opaque conditions. It is possible that the apes acquired the response bias toward the location of the larger quantity in their first choice and persevered in this bias after the transformation of the stimuli, without understanding the invariance of quantities. The response bias might have been triggered by either the simple spatial memory of the larger quantity in the previous setting or by the reflection of their own previous response of pointing at the certain location. Although we cannot totally rule out this possibility in the current study alone, there are two lines of evidence against the repetitive response mechanism. First, the perseveration of the previous response cannot explain the performance of the bonobos and chimpanzees in experiment 2, in which they performed above chance in some condition but not in others (e.g. OS vs. OD in experiment 2). They also seemed to have difficulty especially when the larger quantity was transferred into the tube in both experiments 1 and 2. If they were simply using this strategy, they should have performed equally well across conditions and trial types, but they did not. Second, Call and Rochat (1997) presented their orangutans with a testing condition that was very similar to the OS condition of the current study. The orangutans were presented with a pair of identical clear cups filled with different amounts of juice, which was followed by their first choice. The contents were then transferred into a pair of identical opaque cups in full view of the subjects. The pivot of their procedure is that the locations of the opaque containers were switched in half of the trials before the orangutans were allowed to make their second choice. Three of the four subjects could track the larger quantity at a rate significantly greater than chance in this condition. Perseveration could not be responsible for the performance of these successful apes, because with this strategy the apes should have achieved only 50% success, but this was not the case. Therefore, it is plausible that the repetitive response bias alone cannot fully explain the successful performance of our apes in the current study.

That our subjects likely understood somewhat the invariance of discrete quantities can be also compared with previous reports on apes' numerical skills. Apes are competent with numbers (i.e. addition and subtraction) even with tasks that demand them to use mental representations (e.g. Beran 2001, 2004; Boysen and Berntson 1989; Call 2000). These findings together with our current results nicely fit the Piagetian framework that assumes conservation is a prerequisite for logical reasoning [Piaget 1997 (originally published 1941)].

It should be also added that the current study used relatively small numbers (2 and 5) as test stimuli, and thus investigated the conservation of discrete quantities involving small numbers. Further study is necessary to investigate whether apes can maintain a conservation judgment with

larger numbers. This seems worth exploring because 3- to 4-year-old children are successful at conserving small discrete quantities but fail to do so with large numbers (Gelman 1972; Halford and Boyle 1985). It is possible that apes' understanding of number conservation is constrained in a similar sense. That is, their conservation judgment with respect to discrete quantities could be case-dependent, being influenced by various perceptual factors of stimuli (e.g. the size of quantities, container shape, etc.). Such an incomplete understanding of a conservation concept might constrain apes' numerical operations in terms of accuracy and the size of numbers they can manage.

In conclusion, this study revealed that the conservation of discrete quantities is easier than that of continuous quantities for the bonobos. The results are consistent with the hypothesis that the discreteness of stimuli helps subjects to grasp the consistency of quantities. The chimpanzees and orangutans did not show any evidence supporting this hypothesis, but experimental modifications, such as using comparably attractive food rewards, making the task more demanding, or testing younger subjects and tracking their developmental patterns, are needed to explore whether these species can also benefit from the discreteness of test stimuli in conservation tasks. The study also found that the apes likely possessed some understanding of the invariance of discrete quantities, which is a prerequisite for numerical operations. Further research is necessary to clarify to what extent apes conserve not just discrete quantities but numbers in a genuine sense, resisting sometimes misleading perceptual information.

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