



## Repeated innovation in great apes

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Innovation has been defined as a solution to a novel problem or a novel solution to an old problem. The second part of this definition requires the inhibition of previously learnt solution strategies before a novel solution can be found. Therefore, inventing novel solutions for an old problem is considered to be particularly difficult. We investigated the ability of great apes to produce multiple new solutions to a task after each of those solutions became obsolete. We presented all four nonhuman great ape species with a task consisting of extracting a food reward from a puzzle box. Initially, the task could be solved in three different ways that varied in difficulty. After subjects discovered the first solution, we allowed them to use it for some trials and then it became obsolete. If the apes could overcome their initial response and find the next solution, we again allowed them to use it for some time and once again it became obsolete. The final step consisted of finding the third solution to secure the food reward. We found that all species except orang-utans, *Pongo abelii*, were able to solve all versions of the problem. Furthermore, they overcame the obsolete techniques quickly and efficiently, indicating high degrees of behavioural flexibility and inhibitory control. In contrast to previous research on social learning, our results suggest that great apes are not conservative and adjust their behaviour flexibly when the physical constraints of a task change.

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Prior knowledge plays a fundamental role in innovative problem solving (e.g. Köhler 1925; Epstein et al. 1984). According to Epstein's (1999, page 759) generativity theory novel behaviours or ideas are the 'result of an orderly and dynamic competition among previously established behaviours, during which old behaviours blend or become interconnected in new ways'. This account explicitly highlights the importance of previous experience in order to generate genuinely novel strategies. On the one hand, such previous experience might involve shaped behaviours that lead to novel solutions by an automatic chaining process (Epstein et al. 1984, Epstein 1987). On the other hand, general (i.e. not directly reinforced) experience with objects and their structural properties can be beneficial for solving problems. For instance, Birch (1945) showed that chimpanzees, *Pan troglodytes*, who had a chance to explore an object during free play outperformed subjects without such previous experience in a subsequent test that required the manipulation of that particular object. Whereas chaining can only produce novel solutions on the basis of previously learnt associations, the latter type of knowledge might involve the encoding of structural relations, which enables the subject to adjust its behaviour more flexibly to the task demands (Wertheimer 1959).

Prior knowledge, however, may not always have a positive effect on innovative problem solving; it can also produce mental blockages in the form of Einstellung effects (Luchins & Luchins 1959) or functional fixedness (Duncker & Lees 1945). Recently, Hanus et al. (2011) reported evidence consistent with functional fixedness in chimpanzees in the floating peanut task. In this task, subjects are confronted with an out-of-reach peanut located at the bottom of a vertically oriented tube. The solution to this problem consists of pouring water inside the tube to lift the (floating) peanut off the bottom to get access to it once it reaches the tube opening. Hanus et al. (2011) found that the solution to this problem was facilitated by the introduction of a novel water dispenser. Hanus et al. argued that this may have been caused by the old dispenser having a fixed function (gained by past experience) of supplying drinking water, which would hinder the invention of the novel usage of water. On a more general level, solving a task in one way may hinder the invention of other solutions. Several studies reported such conservatism in chimpanzees in the social-learning domain (Marshall-Pescini & Whiten 2008; Hrubesch et al. 2009; Gruber et al. 2011): once acquired, chimpanzees stayed with their initial solution even though they received repeated demonstration of a more efficient solution. However, it is unclear to what extent this conservatism would also apply when the task constrains change, thus rendering the initial solution obsolete.

Currently, an unresolved question is, what determines the usefulness of prior knowledge? Why does prior knowledge

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sometimes help innovation whereas at other times it blocks innovation in problem solving? Innovation has been defined as 'a solution to a novel problem, or a novel solution to an old one' (Kummer & Goodall 1985, page 203). The first part of this definition might be very different from a cognitive point of view to the second part. Finding a solution to a novel problem often includes applying a previously used solving strategy (or at least parts of it) to the novel problem (transfer task). Therefore, motor routines and/or functional relations gained by previous experience might remain the same. In contrast, finding a new solution to an old problem might require first the inhibition of the old strategy including learnt motor routines and functions of relevant objects such as tools (functional fixedness) before a new solution can be found (inhibition task). Therefore, prior knowledge might facilitate transfer tasks but hinder inhibition tasks. A task that requires subjects to adopt new solutions repeatedly to cope with changing demands, while inhibiting the use of previously successful solutions, appears to be particularly difficult.

In humans and monkeys the associative brain areas, in particular the prefrontal cortex, have been related to executive functions and inhibitory control (Miller & Cohen 2001). However, not all great ape species seem to be equivalent in inhibiting prepotent responses and producing novel, creative solutions. In a detour-reaching task requiring subjects to avoid reaching directly for the food reward, orang-utans, *Pongo abelii*, outperformed chimpanzees, bonobos, *Pan paniscus*, gorillas, *Gorilla gorilla*, and 3–5-year-old human children suggesting superior inhibitory control in orang-utans (Vlamings et al. 2010). Gorillas performed worse than the other great apes on a battery of inhibitory control tasks (Amici et al. 2008). However, such differences have not been detected in other tasks with a strong inhibitory component such as the reverse reward contingency task (Boysen & Berntson 1995; Vlamings et al. 2006; Uher & Call 2008).

Innovation rates have also been positively correlated with the volume of associative brain areas (isocortex and striatum in primates, hyperstriatum ventrale and neostriatum in birds; Lefebvre et al. 2004). Among primates, great apes (especially chimpanzees and orang-utans) show both the highest innovation rates and the largest relative brain size in associative areas. Few studies, however, have investigated innovation from a comparative perspective. One such study has recently been reported by Auersperg et al. (2011): they presented keas, *Nestor notabilis*, and New Caledonian crows, *Corvus moneduloides*, with a puzzle box that initially offered four different options to extract a food reward. Once they mastered one solution that particular solution was blocked. Thus, the birds repeatedly had to abandon a previously used technique to find a new solution. Auersperg et al. found that one (of six) keas and one (of five) crows invented all four solutions, showing significant flexibility in problem solving across these two species of birds.

Orang-utans, chimpanzees and children, unlike gorillas, have been shown to use water as a tool in the floating peanut task (Mendes et al. 2007; Hanus et al. 2011). Orang-utans also outperformed chimpanzees and bonobos in a task that required them to use the shaft of an electrical cable as a straw to extract fruit juice from a container (Manrique & Call 2011). However, there have been no experimental analyses of differences between the four nonhuman ape species with regard to their innovativeness, especially when coping with multiple changes in the apparatus.

The goal of the present study was to investigate the ability of the great apes to produce multiple new solutions to a task after each of those solutions became obsolete. This means that this study assessed not only whether species varied in their ability to produce new responses to meet new task demands but also their ability to refrain from using responses that no longer worked. We presented

all four ape species with a task consisting of extracting a food reward from a puzzle box. Initially, the task could be solved in three different ways that varied in complexity. After subjects discovered the first (easiest) solution, we allowed them to use it for some trials and then it became ineffective. If the apes could overcome their initial response and find the next solution, we allowed them to use it for some time and once again we rendered it obsolete. The final step consisted of finding the third (and final) solution to secure the food reward. Based on the high innovation rates of great apes in the wild compared to other primates (Reader & Laland 2002) we expected significant flexibility and innovation in great apes' problem solving, that is, efficient adjustments in behaviour when the physical constraints of the tasks were changed. Moreover, based on their high innovation and inhibition rates from past studies we expected orang-utans to outperform the other species.

## METHODS

### Subjects

Five chimpanzees, five bonobos, three gorillas and seven orang-utans housed at the Wolfgang Köhler Primate Research Centre (WKPRC) in the Leipzig Zoo participated in this study (see Table 1). There were six males and 14 females ranging in age from 3 to 35 years. Thirteen subjects were mother-reared and seven nursery-reared. Subjects were housed in social groups of 6–18 individuals and spent the day in indoor (175–430 m<sup>2</sup>) or outdoor (1400–4000 m<sup>2</sup>) enclosures, depending on the season. Both enclosures were spacious and equipped with climbing structures, natural vegetation and enrichment devices to foster extractive foraging activity that included the use of tools. Subjects were individually tested (the only exception being mothers with their dependent offspring) in special test cages (5.1–7.3 m<sup>2</sup>) interconnected by lockable doors. The apes were allowed to decide whether to participate or not in our tests. Subjects were not deprived of food. They were provided with fresh fruits, vegetables, eggs, cereals, leaves and meat (once a week) distributed in three main meals (0730, 1330 and 1700 hours). Some more food was dispensed between 0730 and 1330 hours (mainly fresh fruit) and at 1730 hours, as part of the enrichment programme. Water was available ad libitum during testing. The study complied with the European and World Associations of Zoos and Aquariums (EAZA

**Table 1**  
Subjects that participated in the study

Subject	Species	Sex	Age (years)	Rearing history
Fifi	Chimpanzee	Female	16	Mother
Alexandra	Chimpanzee	Female	9	Nursery
Alex	Chimpanzee	Male	8	Nursery
Jahaga	Chimpanzee	Female	16	Mother
Trudi	Chimpanzee	Female	16	Mother
Joey	Bonobo	Male	26	Nursery
Kuno	Bonobo	Male	12	Nursery
Limbuko	Bonobo	Male	13	Nursery
Yasa	Bonobo	Female	11	Mother
Ulindi	Bonobo	Female	15	Mother
Dokana	Orang-utan	Female	18	Mother
Dunja	Orang-utan	Female	35	Nursery
Padana	Orang-utan	Female	11	Mother
Pini	Orang-utan	Female	20	Mother
Bimbo	Orang-utan	Male	28	Nursery
Kila	Orang-utan	Female	8	Mother
Raja	Orang-utan	Female	6	Mother
Kibara	Gorilla	Female	5	Mother
Viringika	Gorilla	Female	14	Mother
Louna	Gorilla	Female	3	Mother

and WAZA) Ethical Guidelines and was approved by the joint ethical committee of the MPI-EVA and Leipzig Zoo.

### Apparatus

The apparatus consisted of a transparent Plexiglas rectangular box (base: 4 cm<sup>2</sup>; height: 28 cm) attached to the cage mesh. A handle attached to the base of the apparatus allowed the subject to lift the bait (i.e. one grape) inside the apparatus 12.5 cm. Three variations of this basic apparatus were presented, each requiring different and gradually more demanding manipulative strategies to obtain the reward. Apparatus 1 had a 4 cm diameter hole drilled on the side facing the subject. The grape inside could be obtained by simply introducing one finger through this hole and reaching down some 12.5 cm (see Fig. 1a), the so-called fingering technique. Apparatus 2 was identical to apparatus 1 except that the hole was located 3.5 cm higher than the hole in apparatus 1. Thus, retrieving the grape required the use of both hands: one to move the handle upwards to displace the reward and the other to reach for the grape (see Fig. 1b), the so-called lifting technique. Apparatus 3 lacked the frontal hole and retrieving the grape required the subject to displace the handle with enough speed to make the grape fly off the apparatus through the opening at the top (see Fig. 1c), the so-called shooting technique. For a photograph of the apparatuses and demonstrations of the techniques used see Fig. S1 and Movies S1–S4 in the Supplementary Material.

The design of the apparatuses was such that the solution required for one apparatus was always viable to solve the previous one, but not vice versa. In other words, although hitting the handle to make the grape fly off was the only suitable solution in apparatus 3, this method was also possible to solve apparatus 1 and 2. However, introducing one finger did not suffice to solve apparatus 3, nor did using both hands, one to hold the handle up and the other to reach for the grape.

### Procedure

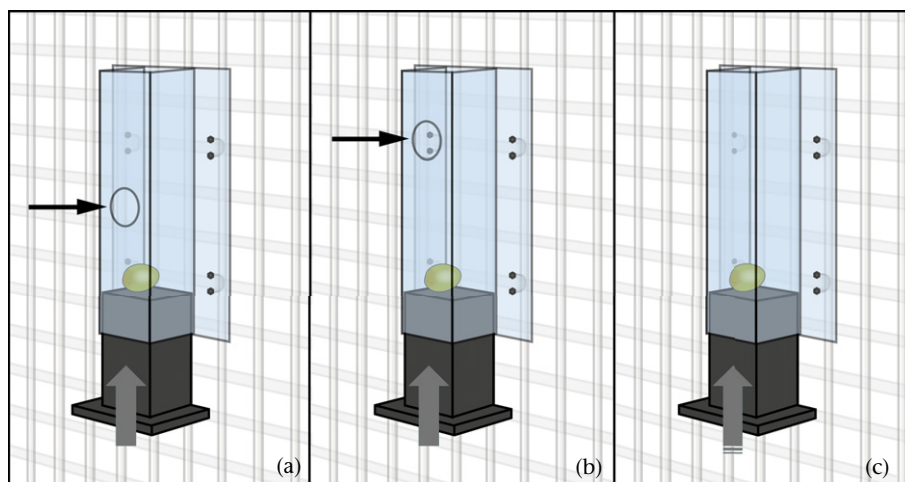
Apparatuses were presented sequentially beginning with the easiest (apparatus 1) and ending with the hardest (apparatus 3). Only subjects who succeeded in one apparatus progressed to the next one. Each session started with the baiting of the apparatus and ended once the subject had retrieved 10 grapes (i.e. 10 trials) or

10 min had elapsed, whichever occurred first. The criterion for advancing to the next apparatus was obtaining 20 grapes in the current apparatus. This means that a minimum of two sessions per apparatus was always necessary. If subjects failed to retrieve the 20 grapes in two consecutive sessions, subjects received additional sessions until they reached the 20-grape criterion. If a subject had not solved the task after five sessions, testing was discontinued and the subject did not advance to the next apparatus.

### Data Scoring and Analysis

All trials were videotaped. Our main dependent variables were success, defined as retrieving the grape, and latency, defined as the time (s) subjects needed to retrieve the first grape in a given apparatus. Only subjects who solved the task obtained a value in this measure. Additionally, we scored the techniques used to attempt to retrieve the grape since it is conceivable that subjects applied the correct technique but unsuccessfully. We distinguished three techniques (fingering, lifting and shooting) corresponding to the least effort action required to solve each apparatus. In particular, we scored fingering when the subject introduced one or more fingers through the apparatus's front hole (which was not possible in apparatus 3). We scored lifting when the handle was moved upwards from its resting position, no matter how high. We scored shooting when subjects hit the handle and made the grape jump off the apparatus floor, no matter how high. The grape could fly 1 cm and land again inside the apparatus or be rocketed out of the apparatus; we coded both events as the same. Scoring of the techniques was exclusive, that is, two techniques could occur at the same time. H.M. scored all trials and C.V. scored 20% of the trials to calculate interobserver reliability, which was excellent for the three techniques coded (Pearson correlations: fingering: 0.91; lifting: 0.95; shooting: 0.98).

We analysed the data using two-tailed nonparametric statistics. We employed the chi-square test to investigate whether the proportion of successful subjects in each apparatus differed between the four species. We used Kruskal–Wallis and Mann–Whitney exact tests to analyse the success and latency across species and to investigate whether the frequency of appearance of each of the three techniques differed between species. Finally, we employed the Wilcoxon signed-ranks test to compare the frequency of the techniques between the last trial of one apparatus and the first trial of the next apparatus.



**Figure 1.** Apparatuses used in the present study. (a) Apparatus 1, (b) apparatus 2, (c) apparatus 3. The hole in the front of apparatus 1 and 2 was accessible to the subjects (marked by the black arrows). All three apparatuses were open on top. The piston at the bottom of all three apparatuses could be pushed upwards (as indicated by the grey arrows). The most prevalent solution for each apparatus was (a) fingering (inserting the finger through the front hole), (b) lifting (pushing the piston upwards and inserting the finger through the front hole) and (c) shooting (forcefully hitting the piston to shoot the grape out through the opening on top).

**RESULTS**

*Apparatus 1*

All subjects except a juvenile gorilla (Louna) solved this apparatus and there were no significant differences between species in the latency to solve it (Kruskal–Wallis test:  $\chi^2_3 = 4.71, P = 0.19$ ; Table 2).

Table 3 presents the percentage of use of the three techniques as a function of species and apparatus. There were significant differences between species in the use of fingering (Kruskal–Wallis test:  $\chi^2_3 = 11.04, P = 0.012$ ) and lifting (Kruskal–Wallis test:  $\chi^2_3 = 10.61, P = 0.014$ ) but no differences in the use of shooting (Kruskal–Wallis test:  $\chi^2_3 = 3.12, P = 0.37$ ). Pairwise comparisons revealed that chimpanzees used fingering significantly more often than gorillas (Mann–Whitney test:  $U = 0, N_1 = 5, N_2 = 3, P = 0.036$ ) and orang-utans (Mann–Whitney test:  $U = 0, N_1 = 5, N_2 = 7, P = 0.003$ ) whereas the reverse was true for lifting: gorillas and orang-utans used lifting significantly more often than chimpanzees.

*Apparatus 2*

All subjects except an adult female chimpanzee (Trudi) solved this apparatus. All successful subjects solved the task using the lifting technique except one adult male orang-utan (Bimbo) who discovered the shooting technique at this stage. There were significant differences between species in the latency to solve this apparatus (Kruskal–Wallis test:  $\chi^2_3 = 8.36, P = 0.039$ ; Table 2). Pairwise comparisons revealed that chimpanzees were slower than bonobos (Mann–Whitney test:  $U = 1.0, N_1 = 4, N_2 = 5, P = 0.032$ ) and orang-utans (Mann–Whitney test:  $U = 1.0, N_1 = 4, N_2 = 7, P = 0.012$ ).

With regard to the technique used, there were significant differences between species in the use of fingering (Kruskal–Wallis test:  $\chi^2_3 = 12.84, P = 0.005$ ) and lifting (Kruskal–Wallis test:  $\chi^2_3 = 8.49, P = 0.037$ ) but no differences in the use of shooting (Kruskal–Wallis test:  $\chi^2_3 = 5.76, P = 0.12$ ). Pairwise comparisons revealed that chimpanzees used fingering significantly more often than bonobos (Mann–Whitney test:  $U = 2, N_1 = N_2 = 5, P = 0.032$ ) and orang-utans (Mann–Whitney test:  $U = 0, N_1 = 5, N_2 = 7, P = 0.003$ ) whereas the reverse was true for lifting: bonobos and orang-utans used lifting significantly more often than chimpanzees.

*Apparatus 3*

Orang-utans performed worse than the other species (Kruskal–Wallis test:  $\chi^2_3 = 9.54, P = 0.023$ ). In fact, none of the six orang-utans tested solved this apparatus (Bimbo who discovered the shooting technique with apparatus 2 was not tested with apparatus

**Table 2**  
Median latency to solve each apparatus as a function of species

Species	Apparatus					
	1		2		3	
	Median	N	Median	N	Median	N
Bonobo	20	5	12	5	621	3
Chimpanzee	24	5	343	4	448	4
Gorilla	106	2	32	2	1469	2
Orang-utan	51	7	25	7	–	0

Only individuals who solved the respective apparatus are included.

**Table 3**  
Median percentage of each technique used as a function of apparatus and species

	Apparatus								
	1			2			3		
	F	L	S	F	L	S	F	L	S
Bonobo	100	0	0	3	93	0	0	24	77
Chimpanzee	100	0	0	27	67	14	1	10	88
Gorilla	5	77	0	0	93	7	0	9	92
Orang-utan	25	71	0	0	100	0	0	100	0

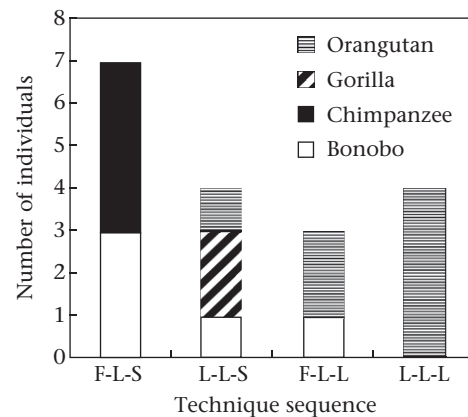
F: fingering; L: lifting; S: shooting.

3) whereas three (out of six) bonobos, all chimpanzees (four) and gorillas (two) did. There were no significant differences in latency between those species that solved this task (Kruskal–Wallis test:  $\chi^2_2 = 0.90, P = 0.64$ ).

There were significant differences between species in the use of lifting (Kruskal–Wallis test:  $\chi^2_3 = 9.93, P = 0.019$ ) and shooting (Kruskal–Wallis test:  $\chi^2_3 = 10.41, P = 0.015$ ) but no significant differences in the use of fingering (Kruskal–Wallis test:  $\chi^2_3 = 7.41, P = 0.06$ ). Pairwise comparisons revealed that orang-utans used lifting significantly more often than bonobos (Mann–Whitney test:  $U = 5, N_1 = 6, N_2 = 5, P = 0.041$ ) and chimpanzees (Mann–Whitney test:  $U = 0, N_1 = 6, N_2 = 4, P = 0.01$ ) whereas the reverse was true for shooting: bonobos and chimpanzees used shooting significantly more often than orang-utans.

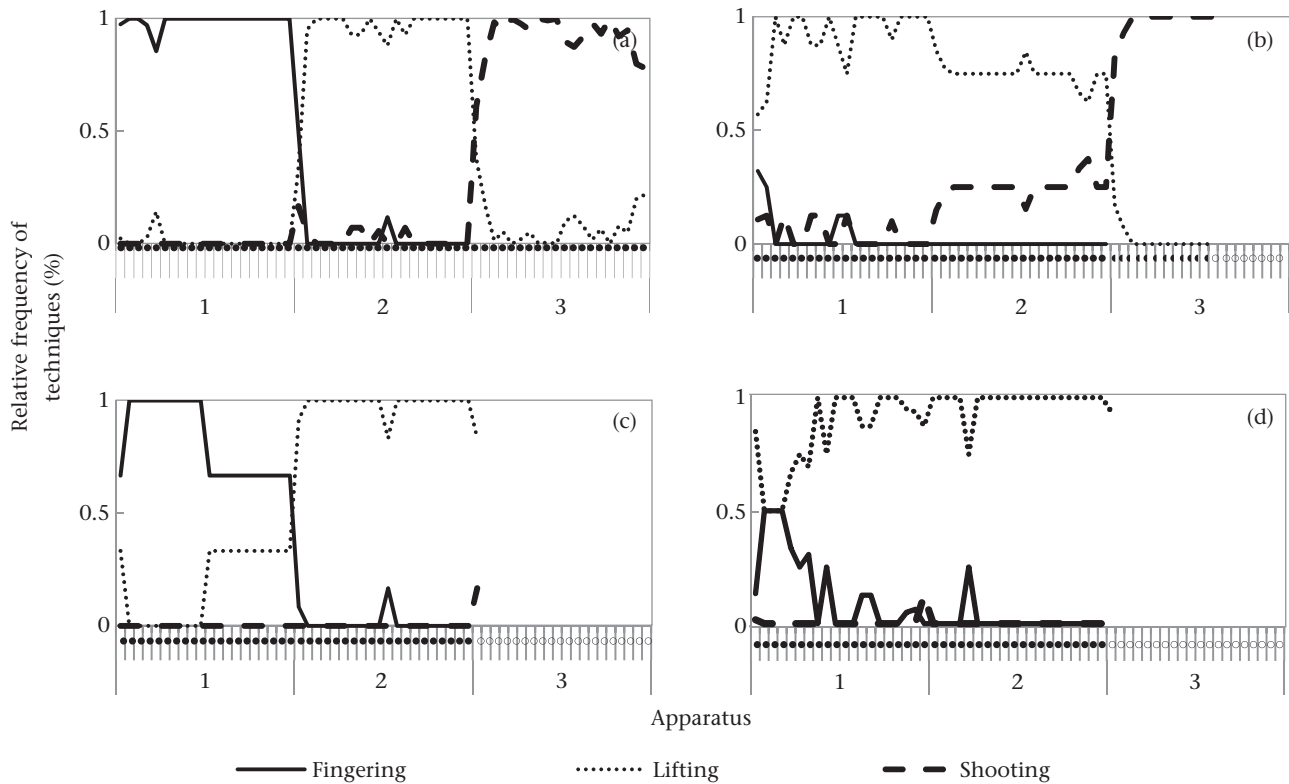
*Transition Between Apparatuses*

Figure 2 presents the number of subjects using each technique. Four chimpanzees and three bonobos displayed all three techniques and switched them as soon as the demands of the new apparatus made that technique obsolete (i.e. fingering, F, then lifting, L, then shooting, S). Two gorillas, one bonobo and one orang-utan began with lifting and switched to shooting at some point (L-L-S). Moreover, two orang-utans and one bonobo began with fingering and eventually switched to lifting (F-L-L). Finally, four orang-utans only used the lifting technique (L-L-L). Figure 3 shows the relative frequencies of techniques used across apparatuses and trials for each group. Particularly noteworthy are the transitions between the apparatuses: there was no gradual transition from one technique to the other; instead, changes in



**Figure 2.** Techniques preferred (simple majority) by each of the individuals to manipulate each of the three apparatuses. Letters represent the type of technique (F: fingering; L: lifting; S shooting) and their order in the sequence of the apparatus to which they were applied.





**Figure 3.** Relative frequency of techniques used as a function of trial and apparatus. Each of the four graphs represents one of the groups defined in Fig. 2: (a) F-L-S, (b) L-L-S, (c) F-L-L and (d) L-L-L. Filled circles underneath the X axis indicate success in  $\geq 67\%$  of subjects on a given trial, semicircles a success rate of  $\geq 33\%$  and  $< 66\%$ , empty circles success in  $< 33\%$  of subjects. Subjects in the groups F-L-L and L-L-L never solved apparatus 3; therefore, no data were available for this apparatus.

techniques occurred suddenly when the old technique became inefficient (except for the L-L-L group, which did not change their initial technique at all).

When contrasting the last trial of apparatus 1 with the first trial of apparatus 2 across all subjects we found that the frequency of the fingering technique was significantly reduced in apparatus 2 compared to apparatus 1 (Wilcoxon signed-ranks test:  $T = 45.0$ ,  $N = 18$ ,  $P = 0.004$ ). The reverse pattern was observed for the lifting technique: more lifting occurred in apparatus 2 compared to apparatus 1 (Wilcoxon signed-ranks test:  $T = 66.5$ ,  $N = 18$ ,  $P = 0.029$ ). Finally, when contrasting the last trial of apparatus 2 with the first trial of apparatus 3 we found significantly reduced lifting in apparatus 3 compared to apparatus 2 (Wilcoxon signed-ranks test:  $T = 66$ ,  $N = 17$ ,  $P = 0.001$ ). Again the reverse pattern was found for the new, efficient technique: shooting occurred significantly more often in the first trial of apparatus 3 compared to the last trial of apparatus 2 (Wilcoxon signed-ranks test:  $T = 66$ ,  $N = 17$ ,  $P = 0.001$ ).

Table 4 shows the frequency of use of the effective techniques right after they became obsolete with the introduction of a new apparatus. In apparatus 2, 10 subjects who discovered lifting did so after a median of three trials using fingering (now obsolete) and they succeeded shortly after that (median = 1.5 trials). In apparatus 3, 13 subjects who discovered the shooting technique did so after a median of five trials using lifting. Five other subjects who did not discover the shooting technique continued to use lifting for a median of 15 trials before giving up their attempts altogether. Of the 13 subjects who discovered the shooting technique, nine eventually succeeded in getting the food whereas four others failed. Successful and unsuccessful subjects required a median of 26 and 46 attempts before succeeding or giving up, respectively. This means that successful

subjects persisted in using shooting for longer than lifting despite the fact that only the latter had been reinforced until that point in time (Wilcoxon signed-ranks test:  $T = 40$ ,  $N = 9$ ,  $P = 0.038$ ).

**Table 4**

Number of responses produced from the moment a technique became obsolete until subjects discovered the new functional technique and the number required to become successful (or to give up) with the new technique

Subject	Species	Apparatus 2		Apparatus 3	
		Obsolescence to discovery	Discovery to success	Obsolescence to discovery	Discovery to success
Fifi	Chimpanzee	10	1	1	5
Alexandra	Chimpanzee	5	1	2	15
Alex	Chimpanzee	6	3	5	26
Jahaga	Chimpanzee	7	2	34	4
Joey	Bonobo	7	6	16	123*
Kuno	Bonobo	0†	NA	2	329
Limbuko	Bonobo	0	1	6	100
Yasa	Bonobo	1	1	0	66*
Ulindi	Bonobo	1	3	11‡	NA
Dokana	Orang-utan	0†	NA	10‡	NA
Dunja	Orang-utan	0†	NA	15‡	NA
Padana	Orang-utan	0†	NA	32	11*
Pini	Orang-utan	0	2	7	26*
Bimbo§	Orang-utan			7	8
Raja	Orang-utan	0	1	35‡	NA
Kila	Orang-utan	0†	NA	15‡	NA
Kibara	Gorilla	0†	NA	3	186
Viringika	Gorilla	0†	NA	1	262

NA: not applicable.

\* No success was achieved.

† The functional technique had already been used in the previous apparatus.

‡ The functional technique was not discovered.

§ Bimbo discovered the shooting technique while working on apparatus 2.

## DISCUSSION

All species succeeded in solving all apparatuses except orang-utans who had problems with apparatus 3. Additionally, chimpanzees were slower than other apes to solve apparatus 2. Species also differed in the techniques that they used for each apparatus. At the beginning of testing (apparatus 1), bonobos and chimpanzees mainly used fingering whereas gorillas and orang-utans predominantly used lifting. Once fingering was eliminated as a viable option (apparatus 2) all species used lifting. Apparatus 3 required another change in technique, something that all species except orang-utans were able to do. In fact, except for one orang-utan (Bimbo) who discovered shooting in apparatus 2, all other orang-utans continued to use lifting in apparatus 3, despite their lack of success. Apes' persistence at using correct actions despite their lack of success contrasts with their quickness at abandoning the use of previously reinforced actions after they became obsolete. Next we discuss these findings in the context of innovative problem solving.

Chimpanzees, bonobos and gorillas were able to solve the hardest problem presented to them, which required forcefully pushing a piston up to make the grape fly out of the apparatus, a solution that no individual produced at the beginning of testing. Moreover, they adopted this technique after having used other techniques to get the grape. This means that they were able to abandon previously successful techniques and innovate to find a new solution.

The finding that chimpanzees needed more time than orang-utans to solve apparatus 2 can be attributed to the fact that, unlike orang-utans and gorillas who already mainly used the lifting technique in apparatus 1, chimpanzees had to invent a new technique to solve apparatus 2 (as their fingering technique was no longer appropriate). Nevertheless, most apes (except orang-utans) overcame their old technique very efficiently once it became necessary, indicating high degrees of behavioural flexibility and inhibitory control (see Fig. 3, Table 4). This was also supported by the analysis of the transition between the apparatuses: the subjects were already able to abandon the previously successful technique in favour of a new one in the first session when task demands changed.

These results contradict previous findings (Marshall-Pescini & Whiten 2008; Hrubesch et al. 2009) showing that chimpanzees tend to stick with their initially learnt technique in a problem-solving situation even though they observed human demonstrators and conspecifics, respectively, using a more efficient strategy. The authors concluded that skill mastery inhibits further exploration and the adoption of new techniques. Here we show, however, that chimpanzees and other great ape species are in fact able to abandon a previously established technique when it is necessary. Thus, chimpanzees' conservatism in the social-learning domain does not apply when changes in the physical constraints of the task make the old techniques obsolete. In the same vein, Lehner et al. (2011) showed that orang-utans were able to change the materials that they used for dipping into a tube containing syrup when the exigencies of the task were altered. As a result of those changes, orang-utans built up more complex dipping techniques, for example using a stick to push a piece of paper down the tube to soak up the syrup. The current results may also be construed as evidence for a cumulative build-up of technology during individual learning since the shooting technique built upon the lifting technique. Recall that the apes invented the shooting technique only when they had some previous experience with the lifting technique. However, it is unclear how readily individuals would copy the complex techniques from others when their own technique is still producing a positive outcome. Recent findings have suggested that the boost of cumulative culture in humans compared to

nonhuman primates might be rooted in sociocognitive capacities rather than general behavioural flexibility (Dean et al. 2012). To summarize, the idea of apes being behaviourally conservative in a food extraction problem seems to hold true when the old behaviour is still totally or partially rewarded. However, if the old behaviour becomes completely inefficient, subjects seem to have no problem abandoning it and searching for a new strategy. This should be considered in future studies in order to shed more light on the topic of apes' behavioural 'conservatism'.

One important issue is the process that was responsible for the invention of the shooting technique. It is very likely that subjects benefited from the visual feedback obtained from the effects of their actions, in particular the effect that moving the piston forcefully up had on the position of the reward with regard to the top opening. Seeing the reward getting closer to the opening may have given them the idea of what to do until they succeeded. Although some may want to equate this process to trial-and-error in the classical sense (Thorndike 1911; Thorpe 1963), we think that conflating the two is a mistake. Trial-and-error is blind to the causal relations between the elements of a problem and it operates only on the outcomes, not on knowledge about the conditions that determine whether outcomes occur or not. Thorndike's cats did not have any insight into the causal mechanisms involved in locking devices (and if they did, Thorndike did not consider it). According to Thorndike, they simply learnt how to open them blindly, without necessarily knowing how they worked. We think that the process here is different. The apes realized what needed to be done to get the grape out of the apparatus and persevered until they succeeded. For instance, one bonobo (Kuno) solved apparatus 3 in the fifth session, yet he already displayed a clear preference for the shooting technique in session 1. Unlike traditional trial-and-error, subjects did not base their learning on getting the reward because its likelihood was too low and therefore their random attempts were not sufficiently reinforced. Such an explanation is supported by the fast and efficient transitions of techniques when the requirements of the task were altered (see Fig. 3, Table 4), even though success often lagged behind. Apes had an idea what to do and persevered in the face of failure until they achieved their goal.

One could argue that even without visual feedback and with enough time, subjects would have succeeded. Taylor & Gray (2009) and Taylor et al. (2010) precisely investigated the effects of visual feedback on problem solving in corvids. They found that New Caledonian crows relied heavily on a perceptual-motor feedback cycle: only individuals that could see the effect of their actions on the reward rapidly succeeded in a string-pulling task. Völter & Call (2012) also investigated the effects of perceptual-motor feedback on problem solving in great apes. They presented one group of apes with an apparatus with visual access of its internal workings so that the apes could see the effects that their actions had on the displacement of the reward. Another group faced the same apparatus but without visual access to the effects of their actions. The results were clear: only those individuals who had visual access to the effects (perceptual-motor feedback) were able to solve the task. This means that even though subjects in the opaque group could have solved the task by (blind) trial-and-error in the classical sense, they did not do so. Note that both groups of individuals operated on the apparatus but only those that got perceptual feedback continued to do so until they found the reward.

This use of ancillary information produced during the course of problem-solving attempts often plays a crucial role in humans. We often do something that does not work, even when we know that it cannot work but the effects that our actions produce help us envisage the correct solution, which we then apply to solve the task at hand. In fact, collecting bits of disparate information to produce solutions is one of the major components of problem solving and

something that may distinguish creative from noncreative individuals (Call, *in press*). Moreover, using bits of information to reproduce a complete solution has been hypothesized to play a major role in some forms of social learning, such as emulation, which are important for the way that apes solve problems. The importance of gathering incomplete pieces of information for problem solving should therefore not be underestimated and not be equated to blind trial-and-error.

A third possible explanation for how subjects solved the most demanding apparatus 3 could fall between blind ‘trial-and-error’ and some ‘insight’ about the apparatus mechanism. More specifically, subjects might have perceived the similarity between the old circular hole of apparatus 2 (now closed off) with the rectangular opening in the top of apparatus 3. Perceptual-motor feedback of the grape getting closer and closer to the top opening after each push may have led to a solution, without requiring a complete understanding of the apparatus’s functioning.

Contrary to our prediction, orang-utans failed to outperform the other species. Unlike most of the African apes, only one of the seven orang-utans was able to solve the hardest problem by making the grape fly out of the apparatus. All other orang-utans continued to use the lifting technique despite its lack of success in apparatus 3. One possible explanation for this failure is that orang-utans lacked enough inhibitory control compared to other apes. However, this argument is weakened by other studies showing that orang-utans are equal to or even better than the African apes with regard to inhibitory control (Vlamings et al. 2006, 2010; Amici et al. 2008). Furthermore, in another study orang-utans were in fact shown to be able to abandon a previously used technique when the exigencies of the task were changed (Lehner et al. 2011). Another possibility, related to the previous one, is that orang-utans’ initial preference for lifting resulted in their using lifting more frequently than the other species, which made it harder to abandon it when it was no longer effective. However, one bonobo and two gorillas that also showed a preference for lifting from the outset of testing were nevertheless able to drop it in favour of the shooting technique as needed.

A third possibility is that the action of slamming the piston or hitting the apparatus in general comes more easily for African apes compared to orang-utans. Note, for instance, that African apes use more pounding actions than orang-utans in gestural communication (Call & Tomasello 2007). Chimpanzees’ predisposition for using pounding actions during extractive foraging also points in the same direction (nut cracking: Sakura & Matsuzawa 1991; Boesch & Boesch-Achermann 2000; pestle pounding: Yamakoshi & Sugiyama 1995). On the other hand, orang-utans explore objects mainly with their mouth, and have shown proficiency in mouth tool manipulation (O’Malley & Mcgrew 2000). In the current study all four chimpanzees tested with apparatus 3 invented the shooting technique, three of them in the first session. In contrast, only three (out of seven) orang-utans ever produced the shooting technique. One of them (Bimbo) solved the problem, while the other two failed. It seems likely then that the greater predisposition of chimpanzees to hit the apparatus gained them additional feedback on the workings of the apparatus. Therefore, the fact that some actions may be more prevalent in some species than in others should not be dismissed. In fact, Manrique & Call (2011) found a reverse pattern between African apes and orang-utans in using straw-like tools to extract juice. In that study, all six orang-utans tested solved the task whereas only one chimpanzee (out of five) and none of the five bonobos did the same. Moreover, additional tests showed that the successful chimpanzee’s knowledge about the functioning of the straw-like tools was more superficial than the orang-utans’ knowledge. Manrique & Call (2011) argued that the difference may be based on the higher propensity that orang-

utans have to manipulate objects and use tools with their mouth. Such a predisposition may have placed them in a privileged position to solve tasks that included a strong oral component. Such a predisposition might also have contributed to orang-utans’ remarkable innovation of using water as a tool to raise the level of a floating peanut (Mendes et al. 2007). Note, however, that in a replication of the floating-peanut paradigm none of the 10 naïve orang-utans tested succeeded whereas seven out of 47 chimpanzees could solve this task (Hanus et al. 2011).

In conclusion, the present results indicate significant flexibility in great apes’ problem solving. In particular, chimpanzees, bonobos and gorillas were not only able to invent different solving strategies but also to abandon a previously established technique rapidly in favour of a new one once the old technique became ineffective. Nevertheless, our sample size was modest and additional data are needed to confirm our findings. Thus, whether orang-utans’ failure to switch techniques was due to some cognitive limitations or whether some inherent predisposition masked their true cognitive abilities cannot be conclusively determined here and will require further research.

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### Supplementary Material

Supplementary material associated with this article is available, in the online version, at <http://dx.doi.org/10.1016/j.anbehav.2012.10.026>.

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