Spontaneous use of tools as straws in great apes

Article *in* Animal Cognition · March 2011

DOI: 10.1007/s10071-010-0355-4 · Source: PubMed

2 authors:

Héctor Marín Manrique
University of Zaragoza

Josep Call
University of St Andrews

Anim Cogn (2011) 14:213–226
DOI 10.1007/s10071-010-0355-4

ORIGINAL PAPER

Spontaneous use of tools as straws in great apes

Héctor Marín Manrique · Josep Call

Received: 21 September 2010 / Revised: 5 November 2010 / Accepted: 15 November 2010 / Published online: 4 December 2010

Abstract Great apes can use multiple tools to extract food embedded in substrates and can invent new ways to exploit those resources. We tested five bonobos, five chimpanzees, and six orangutans in a task in which they had to use (and modify) a tool as a straw to drink the juice located inside a container. Experiment 1 showed that four orangutans and one chimpanzee invented the use of a piece of electric cable to get the juice. Experiment 2 investigated whether subjects could transform a non-functional hose into a functional one by removing blockages that impeded the free flow of juice. Orangutans outperformed chimpanzees and bonobos by differentially removing those blockages that prevented the flow of juice, often doing so before attempting to extract the juice. In Experiment 3, we presented chimpanzees and orangutans with four 3-tool sets (each tool set contained a single straw-like tool) and allowed them to select one tool. Unlike chimpanzees, orangutans succeeded in selecting the straw-like tool above chance levels without having to physically manipulate it. We suggest that orangutans' superior performance is related to their greater reliance on mouth actions during foraging. Experiment 4 investigated whether orangutans were also capable of selecting the suitable tool not by its appearance, but by the effects that it produced. After witnessing the experimenter blow bubbles or absorb liquid with a functional tool but fail to accomplish the same thing with the non-functional tool, orangutans failed to select the functional tool above chance levels.

H. M. Manrique (✉) · J. Call
Max Planck Institute For Evolutionary Anthropology,
Deutscher Platz 6, 04103 Leipzig, Germany
e-mail: hector_manrique@eva.mpg.de

Keywords Problem solving · Innovation · Tool properties · Tool making

Introduction

Innovation has been proposed as one of the major forces allowing individuals to exploit new resources or familiar resources in more effective ways (Sol et al. 2002). Rates of innovation have been associated with executive brain areas in both birds and primates (Lefebvre et al. 1997; Reader and Laland 2002). Moreover, innovation is also correlated with tool use in primates, with great apes achieving the highest scores on both innovation and tool use (Reader and Laland 2002). Indeed, one of the most notable features of ape tool use is its versatility. Chimpanzees in the wild use a variety of tools for a number of foraging activities that include pounding nuts and trees, perforating substrates, and extracting insects, substances and liquids (e.g. McGrew 1992). Tools are also incorporated in other activities such as agonistic and sexual displays, cleaning, and grooming. Similarly, orangutans also use a variety of tools to extract food and/or overcome plant defences (van Schaik and Knott 2001). Tools' manufacture that increases tools' efficiency is another striking behavior observed in great apes as well as other mammals and birds. For instance, Asian elephants (*Elephas maximus*) modify the length of branches that they use to repeal flies (Hart et al. 2001), chimpanzees make brush-tipped tools to extract termites (Sanz et al. 2009) and New Caledonian crows fashion tools to extract grubs (Hunt and Gray 2004).

In captive or semi-captive settings, chimpanzees and orangutans display remarkable creativity in the use of tools (see Beck 1980; Tomasello and Call 1997, for reviews). Indeed, not only apes use a variety of tools to solve a variety of tasks, but they also invent new uses for tools with remarkable regularity. Among the most creative uses observed, there is the use of water to extract a peanut from the bottom of a tube (Mendes et al. 2007). Recently, we witnessed another example of innovative tool use in the course of an experiment devoted to investigate whether subjects could select flexible tools to get access to a juice container located at the end of a 90° shaped tube (Manrique et al. 2010). To be able to dip the tool into the juice, subjects had to select the flexible of three tools displayed on a platform. One of the flexible tools consisted of a 1.2-cm-thick electrical cable formed by three plastic-covered copper strands bound together by an outer white plastic shaft. They received 3 trials in which they could select the cable. Two bonobos selected the cable in one trial, two chimpanzees and one bonobo selected the cable in two trials and one bonobo selected the cable in all three trials. However, they invariably used the cable as we had envisaged. In particular, they dipped and licked the juice off the tool repeatedly. Three orangutans, however, did something different and unexpected. After they had dipped and licked for some trials, just like chimpanzees and bonobos, they invented a new technique that consisted of inserting the cable and using it as a straw by sucking on one end to absorb the juice. The fact that the cable was a novel object for them and that they first tried to dip and lick it to get the juice strongly suggests that we witnessed the invention of a new drinking technique. Next, we report in some detail how each orangutan invented this solution.

An adolescent female (Padana) chose the cable and started dipping and licking off the juice in the first trial. However, after having dipped twelve times (during 147 s), she began to use it as a straw. In the following two trials, she selected the cable again but this time she used it as a straw right away. An adult female (Pini) selected the cable in all three trials. In the first and second trials she dipped and licked the juice off the cable 15 times (143 s) and 16 times (130 s), respectively. In the third trial, she dismantled the cable by pulling the plastic-covered copper strands right away and using the outer cable shaft (now hollow) as a straw. Finally, an adult female (Dokana) used the cable as a straw right away without previously dipping and licking, and she continued to do so in the next two trials.

These observations prompted us to investigate the use of tools as straws in chimpanzees, bonobos and orangutans in more detail. The use of straw-like tools for drinking purposes has been described before (e.g., Osvath and Osvath 2008), but very little is known about the prevalence of invention in the absence of training or the knowledge that individuals have about the features that make a tool functional. With regard to this last issue, studies have shown that apes can select novel tools on the basis of their rigidity (Manrique et al. 2010). In particular, when subjects had to rake a piece of food placed outside of their reach on a platform, they selected rigid tools (and discarded pliable ones) that could transfer enough force to move the food within reach. However, they changed their preference and selected pliable tools when they had to extract liquid (or yogurt) from the bottom of a tube with a 90° angle. Other studies have shown that apes and corvids can select tools based on their size (Chappell and Kacelnik 2002; Mulcahy et al. 2005; Bird and Emery 2009) and capuchins can select pounding tools based on their weight and friability (Visalberghi et al. 2009).

The aim of this study was to investigate whether great apes can spontaneously invent the use of novel tools as a straw to access fruit juice located inside a container (Experiment 1) and if so, whether they would be able to selectively transform non-functional tools into functional ones but leave functional tools unmodified (Experiment 2). Non-functional tools were identical to functional tools except that they had some sort of blockage that prevented the free flow of liquid. The last two experiments investigated whether apes could select suitable tools when given a choice between various options. In particular, Experiment 3 investigated whether subjects needed to manual and orally manipulate the tools (as opposed to visually inspect them) to assess whether they were suitable. Experiment 4 investigated whether orangutans were capable of selecting suitable tools not by their appearance but by the effects that they produced on the environment.

Experiment 1: Spontaneous straw-like drinking

Methods

Subjects

Five chimpanzees (*Pan troglodytes*), six orangutans (*Pongo pygmaeus*), and five bonobos (*Pan paniscus)* housed at the Wolfgang Köhler Primate Research Center (WKPRC) in the Leipzig Zoo participated in this study (see Table 1 for details). There were 5 males and 11 females ranging in age from 8 to 35 years. Nine subjects were mother-reared and 7 nursery-reared. Subjects were housed in social groups of 6–18 individuals and spent the day in indoor (175–430 m^2) or outdoor enclosures (1,400–4,000 m^2), depending on the season. Both enclosures were spacious and naturally designed, equipped with climbing structures and enrichment devices to foster extractive foraging activity that included the use of tools. All tests were conducted in special testing cages (5.1–7.3 m^2) interconnected by lockable doors and they adhered to ethical principles for non-invasive research. The apes were allowed to decide whether to participate or not in our tests. Subjects were provided with fresh fruits,

Table 1 Subjects that participated in the study

Subject	Gender	Age (years)	Rearing history	Experiment participation	Prior experience on tool-use tasks
Chimpanzee					
Fifi	Female	16	Mother		b,d,e,f,g
Alexandra	Female	9	Nursery		d,f
Alex	Male	8	Nursery		d,f
Jahaga	Female	16	Mother		d,e,g
Trudi	Female	16	Mother		d,e,g
Bonobo					
Joey	Male	26	Nursery		b,c,d,e,g
Kuno	Male	12	Nursery		c,d,e,f,g
Limbuko	Male	13	Nursery		c,d,e,g
Yasa	Female	11	Mother		c,d,e,g
Ulindi	Female	15	Mother		b,d,e,f,g
Orangutan					
Dokana	Female	18	Mother		a,b,c,d,e,f,g
Dunja	Female	35	Nursery		a,c,d,e,g
Padana	Female	11	Mother		d,e,g
Pini	Female	20	Mother		a,b,c,d,e,f,g
Bimbo	Male	28	Nursery		a,b,d,e,g
Kila	Female	8	Mother		e,g

a Mulcahy et al. (2005), *b* Mulcahy and Call (2006b), *c* Mulcahy and Call (2006a), *d* Girndt et al. (2008), *e* Martin-Ordas et al. (2008), *f* Martin-Ordas and Call (2009), *g* Manrique et al. (2010)

vegetables, eggs, cereals, leaves, and meat (once a week) distributed in three main meals (7.30 am, 1.30 pm and 5 pm). Some more food was dispensed between 7.30 am and 1.30 pm (mainly fresh fruit) and at 3.30 pm, as part of the enrichment program. Our experiments never interfered with the daily feeding routine. Food and water were also available ad libitum during testing. Subjects had participated in a variety of cognitive studies in which the use of tools was required (see Table 1).

Apparatus

The apparatus consisted of a transparent plastic rectangular box (25 × 10 × 9 cm). When attached to the mesh, a hole of 4 cm in diameter in the subjects' side allowed the introduction of a tool to reach for the grape juice placed inside the box. Two different tools could be tried in this apparatus. One consisted of a gray electric cable measuring (22 × 1.2 cm) formed by five plastic-covered copper strands bundled together by an outer plastic layer (i.e. functional cable). The second tool consisted of the same electric cable whose inner gaps had been sealed with transparent gelatine to prevent for the air and hence the juice, to pass through (i.e. non-functional cable). There were two potential ways of getting the liquid reward; one was by simply dipping the tool in the juice, pulling it out, and licking it. The second way required the subjects to dip the tool and suck on it to bring the juice up as if it were a straw. This second strategy was more efficient because it allowed the subjects to quickly empty the apparatus, but it was only possible with the functional cable.

Procedure

The basic procedure consisted of confronting the subjects with the baited apparatus and providing them with either the functional or the non-functional cable. In order to identify the strategy that subjects used to solve the problem (dip and lick vs. straw drinking), three sessions of three trials were run with the functional cable. Upon completion of these sessions, subjects received 12 additional sessions consisting of six 3-trial sessions with the functional cable and six 3-trial sessions with the non-functional one. The order in which the apes received the functional or the non-functional condition was counter-balanced between subjects. Every session was run in a different day and every trial lasted up to 3 min. In those 3 min, the subject had the chance of emptying the apparatus, provided she used the cable as a straw. With the non-functional cable, she would additionally need to remove the inner copper strands as well as the gelatine. If the box was emptied, the trial was considered over and the next trial started after juice replenishment. If 3 min elapsed without juice consumption, the next trial would automatically start. Subjects could keep the cable from previous trials provided it was intact or in the process of being transformed into a straw. That meant that the tool was only retrieved when it was completely destroyed and thus no longer functioned as a straw, or when it had been already transformed into a perfect functional straw. In these cases, the next trial was conducted with an intact new cable.

Data scoring and analysis

All trials were videotaped. To assess whether subjects were motivated to get the juice, we scored the percentage of trials in which subjects attempted to get the juice by any means. We also scored what method they use to extract the juice in their first attempt. Our main dependent variable, however, was success defined as emptying the apparatus within the allocated time (3 min) which could only be achieved by using the cable as a straw. Our independent variables were the species and the type of tool (functional vs. non-functional). However, during the test we realized that subjects were able to turn non-functional tools into functional ones by bending them. This action apparently fragmented the gelatine and created gaps through which the juice could flow. We calculated percentages of success and analyzed the data using two-tailed non-parametric statistics. Kruskal–Wallis and Mann–Whitney tests were employed to detect variations in success by species. Wilcoxon test was used to evaluate the differences in success by tool type.

Table 2 Percentage of successful trials as a function of the type of tool and species

Subject	Functional ($n = 27$)	Non-functional ($n = 18$)
Bonobo		
Joey	0	0
Kuno	0	0
Ulindi	0	0
Limbuko	0	0
Yasa	0	0
Chimpanzee		
Alex	48.1	100
Trudi	0	0
Jahaga	0	0
Fifi	0	0
Alexandra	0	0
Orangutan		
Bimbo	0	0
Dunja	0	0
Padana	100	94.4
Pini	81.5	100
Dokana	100	–
Kila	100	61.1

Dokana refused to take and use the non-functional tool in every trial. (n) represents the total number of trials implemented in each condition

Results

All species showed great interest in obtaining the juice throughout testing. In particular, orangutans, bonobos, and chimpanzees tried to get the juice in 91%, 84%, and 100% of the trials, respectively. On the other hand, they did not seem interested in dismantling the cable; in fact, only three apes produced a straw (Yasa, Bimbo and Dunja) but they merely used it to dip and lick. All apes dipped and licked the stick in their first attempts to get the juice. Afterward, some apes began to use the cable as a straw. Table 2 presents the percent of successful trials as a function of condition and species. We found no significant effect of condition on success (Wilcoxon test: $Z = 0.36$, $P = 0.71$). In contrast, species differed significantly in their success (Kruskal–Wallis tests: $\chi^2_3 = 6.51$, $P = 0.039$). Pairwise comparisons revealed that orangutans were more successful than bonobos (Mann–Whitney test: $Z = 2.11$, $P = 0.03$). In contrast, there were no significant differences between the other species (Mann–Whitney tests: chimpanzee-orangutan: $Z = 1.79$, $P = 0.07$; chimpanzee—bonobo: $Z = 1$, $P = 0.32$). However, three orangutans discovered that the cable could be used as a straw in the first trial of the first session and an additional orangutan did so in the third trial of the second session. Only one chimpanzee (Alex) used the cable as a straw (in the third trial of the fifth session), and no bonobos discovered the use of the cable as a straw.

Discussion

Four out of six orangutans spontaneously used the cable as a straw during this experiment. Although their first attempts to get the juice consisted of dipping and licking the cable, they quickly began to use the cable as a straw never to return to the less efficient dip and lick technique. In contrast, bonobos never discovered this more efficient technique. Chimpanzees did not fare much better since only one individual used the cable as a straw, and it took him 15 trials to make the discovery. The two orangutans (Dunja and Bimbo) that failed to solve the task were also the oldest, 35- and 28-year old, respectively. Additionally, Alex, the only chimpanzee succeeding, was the youngest in his group. We do not think that the age accounts for the orangutans' better performance because it is fairly evenly distributed in the three samples tested (see Table 1); however, it could still play an important role in preventing or delaying the appearance of new solutions.

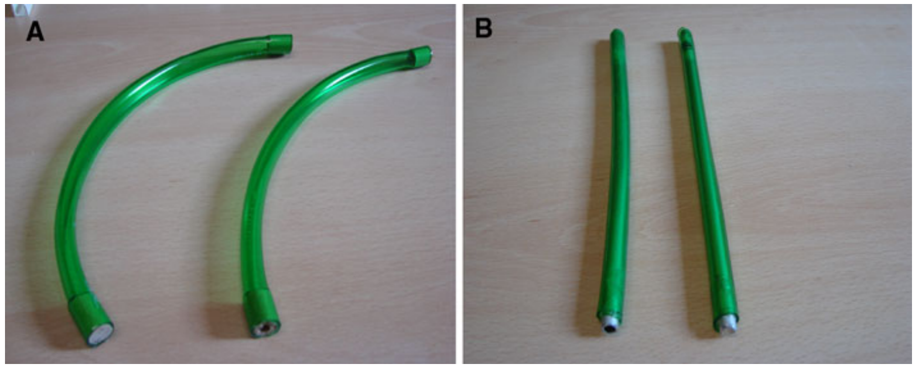

Fig. 1 Depicted the functional and non-functional exemplars corresponding with the *dowel* (Panel **a**) and the *bar* (Panel **b**) tasks employed in Experiment 2. The hollow exemplar in each set represents the functional tool

The remarkable superiority of orangutans over the two other species in this task cannot be explained by a lack of motivation by part of the chimpanzees and bonobos; otherwise, a decrease in dipping intensity would be observed throughout the session and that was never the case for any of the subjects participating. One possible explanation for the difference between species may be related to orangutans' strong preference toward manipulating the cable with their mouth. This manipulative preference, which has already been described in another tool-using context by O'Malley and McGrew (2000), could put them one step closer to the straw-like solution than the other two species. Nevertheless, it is still remarkable that they acquired the straw drinking technique so quickly and more so when these same subjects were indeed reinforced for using stick-like tools to dip and lick off liquid reinforcers in a previous study (see Manrique et al. 2010). Although they used dip and lick in their initial attempts, they quickly dropped this inefficient approach for the more efficient straw-drinking technique.

Finally, the tool type did not influence subjects' success in the task but this conclusion needs to be taken with great caution because, as we mentioned earlier, orangutans managed to change the non-functional into a functional tool. Although this was one of the goals of this experiment, it is unclear whether they did this on purpose or simply was a by-product of their general manipulative activity. Originally, we had envisaged a solution that consisted of removing the copper cables and using the outer plastic skin as a fully functional straw but orangutans found another solution that consisted in inserting the cable in the apparatus and bending it. In the next experiment, we attempted to address the question of straw production once more by presenting a new set of tools. In this case, however, non-functional exemplars were completely ineffective unless subjects removed the blockages that prevented the juice flow.

Experiment 2: Transforming non-functional tools into functional straws

Methods

Subjects

We used the same subjects that participated in Experiment 1 but we dropped the bonobos after completing the dowel task because they displayed no indication of straw-like drinking behavior.

Apparatus

We used the same apparatus as in Experiment 1 except that we changed the tools. There were two tool sets corresponding to two tasks. In the dowel task, the tools consisted of a rubber green hose (22 × 2 cm) whose ends were blocked by two wooden dowels (3 × 2 cm). The dowels of the functional tool had a 0.5-cm orifice that allowed the flow of juice whereas those of the non-functional tool had no orifice (see Fig. 1). Both dowels were inserted while keeping the hose under boiling water to make them really tight thus avoiding their accidental removal. In the bar task, the tools consisted of the same green hose of the dowel task except that we inserted a gray metal bar (22 × 1.8 cm) into the tube (see Fig. 1). In the functional condition, the bar was hollow whereas in the non-functional condition the bar was solid. Again the bar was inserted inside the tube while keeping the hose under boiling water thus resulting in a tight fit.

Procedure

We used the same basic procedure as in Experiment 1. Namely, we confronted the subjects with the baited apparatus and provided them with either the functional or the non-functional tool to gain access to the juice. However, the total number of sessions was reduced to six for each tool set. Three 3-trial sessions were run with the functional tool and three more with the non-functional one. The order in which subjects received the functional and the non-functional tools stayed the same as in Experiment 1. All subjects received the dowel task first and the bar task second. Every session was run in a different day and every trial lasted up to 3 min. In those 3 min, the subject had the chance of emptying the apparatus, provided she used the tool as a straw. With the non-functional tool, an additional operation was required: removing the two wooden lids (dowel task) or the metal bar (bar task) before using the hose as a straw. In both experiments, any trial was considered over as soon as the subject consumed the juice. If 3 min had elapsed without juice consumption, the next trial automatically started. Subjects kept the tool from previous trials provided it was intact or in the process of being transformed into a straw. This means that it was only retrieved when it was completely destroyed and thus no longer could function as a straw, or when it had been already transformed into a perfect functional straw. In these cases, the following trial would start with an intact new tool. There were trials in which we could not retrieve the old tool and the individuals had to start the following trial with the same tool. These trials were excluded from our analysis if the tools had been already modified. Since these trials represented only 6.4% of the cases, we reasoned that their exclusion represented no significant loss of information.

Data scoring and analysis

Data scoring and analyses were identical to those of Experiment 1 except that we also scored as a dependent measure the percentage of trials in which tool modifications occurred defined as removing the necessary blockages from the tools to turn a non-functional tool into a functional one. This involved removing one and two blockages in the bar and dowel tests, respectively. Additionally, we scored the percentage of trials in which the modification occurred prior to inserting the tool into the box juice for the first time.

Results

Dowel task

Table 3 presents the percentage of successful trials as a function of condition and species. We found no significant effect of condition on success (Wilcoxon tests: $Z = 0.53$, $P = 0.59$). In contrast, success significantly differed between species (Kruskal–Wallis tests: $\chi^2_3 = 11.67$, $P = 0.003$). Pairwise comparisons revealed that orangutans were more successful than bonobos (Mann–Whitney

Table 3 Percentage of successful trials and modified tools as a function of the type of tool and species in the dowel task

Subject	Successful trials		Modified tools	
	Functional ($n = 9$)	Non-functional ($n = 9$)	Functional ($n = 9$)	Non-functional ($n = 9$)
Bonobo				
Joey	0	0	0	0
Kuno	0	0	0	0
Ulindi	0	0	33.3	100
Limbuko	0	0	88.9	22.2
Yasa	0	0	100	57.1
Chimpanzee				
Alex	100	77.8	0	66.7
Trudi	0	0	0	0
Jahaga	0	0	0	0
Fifi	0	0	0	11.1
Alexandra	0	0	33.3	77.8
Orangutan				
Bimbo	44.4	100	77.8	100
Dunja	77.8	0	100	100
Padana	100	100	0	100
Pini	100	100	11.1	88.9
Dokana	100	100	0	100
Kila	100	100	11.1	100

(n) represents the total number of trials implemented in each condition

Table 4 Percentage of successful trials and modified tools as a function of the type of tool and species in the bar task

Subject	Successful trials		Modified tools	
	Functional ($n = 9$)	Non-functional ($n = 9$)	Functional ($n = 9$)	Non-functional ($n = 9$)
Chimpanzee				
Alex	100	0	0	0
Trudi	0	0	0	0
Jahaga	0	0	0	0
Fifi	0	0	0	0
Alexandra	0	0	0	0
Orangutan				
Bimbo	88.9	88.9	11.1	77.8
Dunja	88.9	88.9	88.9	100
Padana	100	66.7	0	66.7
Pini	100	100	0	100
Dokana	100	100	0	77.8
Kila	100	22.2	0	0

(n) represents the total number of trials implemented in each condition

test: $Z = 2.95$, $P = 0.003$) and chimpanzees (Mann–Whitney test: $Z = 2.49$, $P = 0.013$). In contrast, there were no significant differences between bonobos and chimpanzees (Mann–Whitney test: $Z = 1.00$, $P = 0.32$).

Table 3 also presents the percentage of modified tools as a function of condition and species. Subjects were significantly more likely to modify the tool in the non-functional than the functional condition (Wilcoxon test: $Z = 2.18$, $P = 0.029$). When considering species separately, neither bonobos' (Wilcoxon tests: $Z = 1.07$, $P = 0.28$) nor chimpanzees' (Wilcoxon tests: $Z = 1.60$, $P = 0.11$) tool modification was influenced by condition. In contrast, orangutans modified tools more often in the non-functional than the functional condition. (Wilcoxon tests: $Z = 2.06$, $P = 0.03$).

Bar task

Table 4 presents the percentage of successful trials as a function of condition and species. We found no significant effect of condition on success (Wilcoxon tests: $Z = 1.60$, $P = 0.11$). Orangutans significantly outperformed chimpanzees (Mann–Whitney test: $Z = 2.82$, $P = 0.005$). Moreover, orangutans modified tools more often in the non-functional compared to the functional condition (Wilcoxon tests: $Z = 2.03$, $P = 0.04$). Chimpanzees modified no tools in this task.

Next, we pooled together the data for both tasks and analyzed the timing of the tool modification in relation to the first tool insertion in each trial. Alex never modified the tool prior to its use. In contrast, orangutans on average modified the non-functional tool in 69.8% of the trials (range: 44–100%) prior to its insertion. That is, they modified the tool prior to its use. However, three of the orangutans also modified the functional tool in 100% of the trials, even though it was not necessary. Restricting the analyses to those orangutans who did not modify functional tools (see Tables 3 and 4), revealed that on average they modified the tool prior to its use in 47% of the trials (range: 44–50%).

Discussion

Orangutans outperformed bonobos (dowel task) and chimpanzees (dowel and bar tasks) in using a tool as a straw to drink juice from a box. Orangutans modified tools more often than the other species and tool modifications often occurred before subjects attempted to get the juice and failed. Additionally, orangutans were more likely to modify non-functional compared to functional tools. It is conceivable that there could be an efficiency gain derived from removing the blockages from the functional tools. However, this gain would have been minimal because subjects were able to very quickly empty the contents of the container with the functional tool as a straw even with its 'blockages' in place.

The orangutans' success in both tasks replicated the results of Experiment 1. In fact, their success increased by 20% because two additional orangutans, which also participated in Experiment 1, discovered how to use the tool as a straw during the course of the current experiment. Bimbo discovered its use in the third trial of session 17 and Dunja in the third trial of session 19. That these two individuals were also the oldest ones in the study (28 and 35 years old, respectively) makes this finding particularly remarkable, more so if we consider that all apes were tested alone and they never faced any experiment involving straw use before. In contrast with the orangutans' success, no bonobo and only one chimpanzee ever used the tool as a straw, not even when the functional hose was handed. Although one could argue that Alex may have succeeded because he was nursery-reared and presumably had more experience with human artefacts, other chimpanzees and bonobos who were also nursery-reared did not make this discovery.

Orangutans also differed from the other species in that they routinely transformed the non-functional hose into a functional straw in both tasks by removing the blockages that impeded the passage of juice. Such transformation occurred much less frequently when provided with functional tools. Overall, subjects removed 84% the blockages from non-functional tools compared to only 23% of the blockages in functional tools. Bimbo and Dunja deserve a special mention. Both needed a minimum of 51 trials before discovering how to drink straw-like; throughout these sessions they showed a strong tendency toward completely dismantling the tools before even trying with the juice box, and when they first discovered that the tool could be more efficiently used as a straw, both lids had been already removed. From then on, they dismantled the tool as soon as they had it and that could explain why they never came to differentiate the functional and the non-functional tool.

We observed a clear difference in tool transformation between the two tasks. In the dowel task, orangutans removed 100% of the blockages of the non-functional tools but only 28% of those of the functional tools. In the bar task, orangutans removed 68% of the blockages of the non-functional tools but only 17% of those of the functional tools. Thus, orangutans transformed more non-functional tools into functional ones in the dowel task (100%) compared to the bar task (68%). It is very likely that this difference reflects the greater difficulty in transforming the tool in the bar task. We witnessed how the subjects struggled with the non-functional tools, sometimes for almost the whole 3-min trial period. The youngest orangutan (Kila) never managed to completely remove the bar, despite trying without pause for the whole session. It is conceivable that bar removal required some sort of technique, other than brute force, that she seemed to lack. Alex's lack of success may reflect similar problems with bar removal but unlike the orangutan he gave up almost immediately on tool modification and changed to the basic dip and lick technique.

Orangutans transformed non-functional tools prior to their use in 54 and 68% of the trials of the dowel and bar task, respectively. In contrast, Alex, the only chimpanzee that modified the non-functional dowel tool never modified it prior to using it. Although one could argue that the percentage of trials in which orangutans dismantled the non-functional tool prior to its use was not that high, one has to consider that the cost of inserting and trying first unmodified tool was almost insignificant in terms of both time and effort. In only a few seconds, the subjects could introduce the tip of the tool and discover right away whether it was functional. The fact that they dismantled the non-functional tool exemplars in the majority of trials prior to introducing them in the box suggests some knowledge about the critical features that may make a tool functional. In the next two experiments, we probed this knowledge further by investigating whether subjects could use visual information about the features (Experiment 3) or functions (Experiment 4) of tools to make a correct tool selection.

Experiment 3: Selection based on perceptual features

Methods

Subjects

We tested the same orangutans and chimpanzees as in Experiment 2 (see Table 1). We excluded the bonobos because none of them ever displayed straw-like tool use in any of the previous experiments.

Apparatus

We used the same apparatus as in Experiment 1 except that we changed the tools. There were four tool sets, each composed of three tools. The tools (all 22 cm long) differed in color, material, diameter, and, critically, hollowness (see Fig. 2 for details). Only one tool in each set allowed the flow of liquid. We presented each set of tools on a sliding platform perpendicular to a Plexiglas panel with three holes (left, center, and right). We placed each tool in front of each hole, perpendicular to the panel and parallel to the other tools, separated from each other by 29 cm. The platform with the tools and the box containing the juice were placed next to each other outside the subject's cage (see Fig. 3 for details), and hence, the subject had visual access to both at the time she made her choice.

Procedure

The basic procedure consisted of confronting subjects with the baited apparatus and offering them to pick one of the three tools to gain access to the liquid reward. Prior to selecting one of the tools, the subject received one of two types of information about the tools corresponding to the following two conditions:

Manipulation The experimenter introduced the three tools inside the subjects' cage so that she could freely manipulate them. Once subjects stopped manipulating the tools, we retrieved them and placed them on their pre-

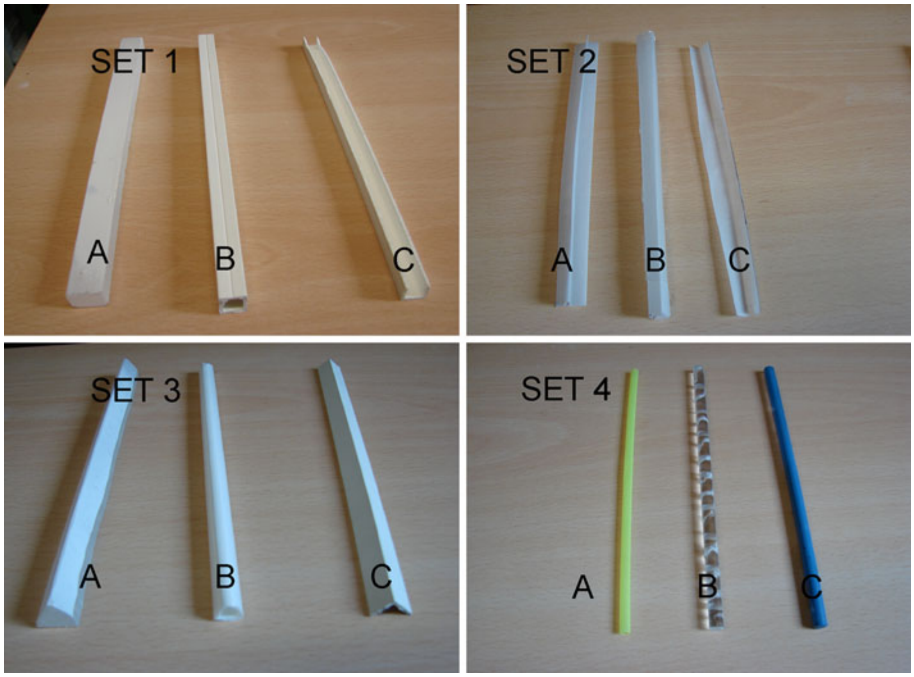

Fig. 2 Tool sets used in experiment 3. All tools were 22 cm long; the word hollow identifies the functional exemplar in each set. Set 1: *A White rectangular-shaped* Plexiglas bar, 1.6 × 1 cm; *B white and hollow square* plastic stick, 1.2 × 1.2 cm and *C* white *U-shaped* plastic stick, 1.2 × 0.9 cm. Set 2: *A* white *T-shaped* paper stick, 1 cm side length; *B hollow pentagon-shaped* paper stick, 1 cm side length and *C white bended* paper stick 3 cm wide. Set 3: *A white triangular-shaped* Plexiglas stick 1.9 cm side length; *B white and hollow triangular-shaped* plastic stick, 1.1 cm side length and *C white V-inverted-shaped* plastic stick, 1.1 cm side length. Set 4: *A* thin and *hollow yellow plastic straw*, 0.6 cm in diameter; *B* Wrinkled transparent Plexiglas stick, 0.85 cm in diameter and *C* Smooth *blue* Plexiglas stick, 0.85 cm in diameter (color figure online)

Fig. 3 Setup of experiment 3. Depicted the three tool alternatives and the juice-baited box

assigned locations on the platform. During tool manipulation, a thin transparent plastic panel prevented the subjects from inserting the tools into the juice-baited box.

Observation The experimenter placed the three tools on their pre-assigned locations on the platform, called the subject's attention, and manipulated the tools for about 10 s each. The manipulation consisted in turning the tool so that the subject could see every side of the tool at least once and could therefore detect the critical information regarding the hollowness of each tool.

Once the tools were in their designated locations, the experimenter closed his eyes and waited 3 s before pushing the sliding platform forward for the subjects to choose. Only one choice was permitted. All subjects received both the manipulation and the observation conditions in different days with the order of presentation counterbalanced across subjects; that is, half of the subjects received the manipulation condition first and the other half received it second. Subjects received one condition per day in two consecutive days. Each day was composed of four trials (2 trials per tool set). Thus, overall, subjects received 8 test trials (4 manipulation and 4 observation). We also counterbalanced the position of the tools within each set across trials so that the hollow tool appeared the same number of times in the left, middle, and right positions.

Data scoring and analysis

We videotaped all trials and scored whether the subject chose the straw-like tool. Our dependent measure was the percentage of trials in which the subject selected the straw-like tool. We analyzed the data using two-tailed nonparametric statistics. We used the Mann–Whitney test to analyze the effect of order of presentation and species on the percentage of correct responses. The Wilcoxon test was used to asses whether subjects selected the correct tool more than would be expected by chance ($P = .33$).

Results

There was no significant effect of the order of presentation in the Observation (Mann–Whitney test: $Z = 0.19$, $P = 0.85$) or the manipulation condition (Mann–Whitney test: $Z = 1.61$, $P = 0.11$). Therefore, we collapsed the data across order of presentation for all subsequent analyses. Table 5 presents the percentage of trials in which subjects selected the correct tool as a function of condition and species. There was no significant difference between conditions (Wilcoxon test: $Z = 0.06$, $P = 0.95$).

Overall, orangutans tended to select the correct tool significantly more often than chimpanzees (Mann–Whitney test: $Z = 1.94$, $P = 0.052$). In fact, orangutans selected the correct tool above chance levels both in the manipulation (Wilcoxon tests: $Z = 2.00$, $P = 0.045$) and in the observation conditions (Wilcoxon tests: $Z = 2.25$, $P = 0.024$). In contrast, chimpanzees performed at chance level in both conditions (Wilcoxon tests: manipulation: $Z = 0.41$, $P = 0.68$; observation: $Z = 0.14$, $P = 0.89$). However, if we restrict our analysis of the orangutan data to the first trial of each set, their performance was not above chance levels for any of the two conditions (Wilcoxon tests: $Z < 1.59$, $P > 0.11$ in both cases).

Discussion

Orangutans performed better than chimpanzees and were able to select the correct tool above chance levels in both the manipulation and observation conditions. This means that they did not solely rely on aspirating air through the tube to select correctly but they could also use visual cues to guide their selection. This seems quite remarkable given that the tools were completely unfamiliar to the subjects and they only had approximately 20 s to examine them before choosing. Their preference for the straw-like tool, however, was not strong enough to allow them to select above chance levels in the first trial even though their score here was not that different from their overall score.

Chimpanzees failed to select the straw-like tool more frequently than would be expected by chance, which is exactly what we predicted based on their previous performance. Alex, the only chimpanzee who discovered the straw-like technique in the previous experiments, showed a mixed performance. Whereas he was able to select the suitable tool in all four trials of the manipulation condition he failed to do so in the four trials of the observation condition, suggesting that his choices relied on what the tools felt like rather than on what the tools looked like.

Although the current experiment established that orangutans could select tools based solely on the perceptual features, it did not inform us about whether these features were taken merely as a cue that predicted success or failure or were processed also in terms of the function that they could accomplish. Perceptual and functional features usually covary but these two types of information can be potentially dissociated. In the next experiment, we employed tool exemplars that were perceptually identical but differed in their functionality and investigated whether tools that had shown their functionality would be preferred over those that had not done so.

Table 5 Percentage of correct selections (all and 1st trial) as a function of condition and species in Experiment 3

Subject	Manipulation		Observation	
	All trials ($n = 4$)	1st trial ($n = 2$)	All trials ($n = 4$)	1st trial ($n = 2$)
Chimpanzee				
Alex	100	100	0	0
Trudi	25	50	0	0
Jahaga	25	0	100	100
Fifi	50	50	25	0
Alexandra	25	50	50	50
Orangutan				
Bimbo	100	100	50	50
Dunja	75	50	100	100
Padana	50	50	50	0
Pini	75	50	100	100
Dokana	100	100	100	100
Kila	25	0	50	50

(n) represents the total number of trials implemented in each condition

Experiment 4: Selection based on function

Methods

Subjects

We used the chimpanzee Alex and the same orangutans that participated in Experiment 3, except for Dunja that became ill and died at the time this experiment started (see Table 1).

Apparatus

The apparatus consisted in the same transparent plastic rectangular box employed in the previous experiments. Two identical gray plastic tubes (22 cm × 1 cm) were the only two alternatives that subjects could pick in this experiment. One of the tubes was hollow and could be used as a straw while the other tube was filled with transparent glue and hence could not be used as a straw. The tool exemplars were presented on the sliding platform in the same manner previously described, except that the separation was increased to 58 cm to match the two extreme holes in the Plexiglas panel. Once deposited on the platform, the two tool alternatives looked identical and it was impossible for the subjects to tell them apart. We also used two 250 cc glasses 1/3 filled with tomato juice, cereals, and Styrofoam balls to provide a demonstration of the functional properties of the tools. Additionally, we reused two tools belonging to the fourth set of Experiment 3 (see Fig. 2) to run four pre-test trials. One worked as a straw (yellow plastic straw) and the other did not (blue Plexiglas tube).

Procedure

Subjects received a total of 8 test trials divided in two different sessions. Every session started with two pre-test trials in which subjects had to choose between the two familiar exemplars corresponding with tool set 4 of Experiment 3. These pre-test trials were only intended as a warm-up and were administered following the same procedure used in the observation condition of Experiment 3. After completing this warm-up phase, subjects advanced to the test phase in which four additional trials were run, each preceded of a demonstration of the tool properties. Because the two tools to choose from remained constant throughout the whole testing phase and what changed here was the demonstration performed with them, we indicate each different type of demonstration. Therefore, every session was composed of two warm-up trials followed by 4 test trials (two trials per demonstration type). During a test trial, each of the two tools was placed on the platform in front of the two holes in the Plexiglas panel. Next to the tools were some other materials that took part in the demonstration (see below). After a demonstration with each tool, the experimenter repositioned the tools in their original positions. Upon concluding the demonstration on both tools, the experimenter removed any remaining objects from the platform (except for the tools), closed his eyes and waited for 3 s before pushing the sliding platform forward for the subjects to choose one of the tools. Two consecutive trials interspersed by the demonstration were run switching tool positions. We administered the following four demonstrations:

Drinking Two 250 cc glasses were placed right besides each tool 1/3 filled with tomato juice. After calling the subject's attention, the experimenter grabbed the functional tool and drank the juice in two bouts, every bout being followed by a 5 s pause. After he finished the juice, the experimenter replaced the tool on the platform and took the non-functional tool, put it in his mouth and attempted to drink the juice as before. This time, however, nothing happened. Since this condition could be less salient than the other one in which the juice vanished, the experimenter hit the glass with the non-functional tool for 5 s following every bout to produce some noise.

Bubble making Again we placed the two glasses with juice on the platform and the experimenter introduced an end of the functional tool into the tomato juice and blew twice to produce bubbles, with every blowing bout being followed by a 3-s pause. Next, the experimenter introduced the end of the non-functional tool into the tomato juice and attempted to blow twice, every bout followed by 3 s in which E stirred the juice with the tool.

Cereal sucking We placed three grains of chocolate cereal next to each of the tools. The experimenter used the functional tool to suck each of the grains in three bouts, each followed by a 2-s pause. Next, he attempted the same with the non-functional tool but failed and threw the cereal grains off the platform by hitting them with the tool.

Styrofoam blowing We placed fifteen yellow Styrofoam balls (diameter = 0.5 cm) spread around each of the tools. The experimenter took the functional tool and blew off the Styrofoam balls that surrounded the tool in two bouts, each bout followed by a 3 s pause. With the non-functional tool exemplar, the experimenter attempted to blow over the Styrofoam balls but nothing happened. After every blowing bout, he swept half the Styrofoam balls off the platform with the tool.

The drinking and blowing bubbles demonstrations took place in the first session whereas the cereal sucking and Styrofoam blowing demonstrations took place in the second session.

Data scoring and analysis

We videotaped all trials and scored whether the subject chose the functional tool. Our dependent variable was the

Table 6 Percentage of correct selections (for each set and overall) as a function of condition and species in Experiment 4

Subject	Sucking		Total	Blowing		Total
	Set 1 ($n = 2$)	Set 3 ($n = 2$)		Set 2 ($n = 2$)	Set 4 ($n = 2$)	
Chimpanzee						
Alex	0	0	0	50	50	50
Orangutan						
Bimbo	50	100	75	50	50	50
Padana	100	50	75	50	50	50
Pini	50	0	25	100	50	75
Dokana	50	50	50	50	50	50
Kila	50	100	75	0	0	0

(n) represents the total number of trials implemented with each tool set

percentage of trials in which subjects selected the functional tool. We used the Wilcoxon test to asses whether subjects selected the correct tool more than would be expected by chance ($P = .50$). We also used the Friedman test to compare the percent of correct trials across demonstrations.

Results and discussion

Table 6 presents the percent of correct trials in each condition. Overall, subjects did not significantly select the functional tool above chance levels (Wilcoxon tests: $Z = 0.38$, $P = 1$). Additionally, there was no significant difference in the percentage of correct trials across demonstration conditions (Friedman test: $\chi^2 = 0.23$, $P = 0.97$). Consequently, we found no evidence that subjects used the effect generated by each of the tools on the demonstration materials to select the functional tool.

General discussion

All orangutans discovered the use of tools as straws during the course of the study, and they were able to remove blockages that turned non-functional into functional tools. Blockage removal was mainly targeted at non-functional tools and three of the orangutans removed the blockages before they even tried to use the tools. In selecting tools, they did not need to manipulate the tools prior to be able to pick the suitable one. That is, they did not need to suck air through the tool to select it but they failed to use the effects created by functional tools on the environment to select the functional tool. In contrast to the orangutans, none of the bonobos and only one of the chimpanzees discovered the use of tools as straws. Unlike orangutans, however, the successful chimpanzee never modified a non-functional tool prior to its use and he needed to manipulate the tools to be able to select the appropriate one.

Although all the species investigated in the current study are considered to be innovative, we found important differences between orangutans on the one hand, and bonobos and chimpanzees on the other. One reason for this difference may be that the task demands fit the orangutans' behavioral propensities more closely than those of the other species. In particular, orangutans are known to explore objects with their mouth, and have been observed to manipulate tools with their lips with great proficiency (Fox et al. 1999; O'Malley and McGrew 2000). This is not surprising if one considers that orangutans are a highly arboreal species whose hands may be occupied in supporting a large body size while foraging in the canopy. A stronger reliance on mouth manipulation may be an adaptation to arboreal life (O'Malley and McGrew 2000) in the same way that knuckle-walking is an adaptation to terrestrial locomotion in the African apes. Thus, it is conceivable that the inter-specific differences observed in this study may not solely reflect a difference in innovation tendencies but additionally, they reflect the behavioral propensities of each species.

Our tentative conclusion on species differences has to be taken with caution because our sample size is relatively small and future studies should attempt to replicate our results with more individuals. Moreover, our results should not be taken as evidence that chimpanzees and bonobos are unable to invent the use of straws. In fact, one of the chimpanzees tested did invent the use of the electrical cable as a straw and later on used other straw-like tools effectively to extract the juice. Moreover, he even modified non-functional tools to make them functional. Nevertheless, he was not as flexible as some of the orangutans since he did not anticipate the effect of blockages prior to using the tool and needed mouth exploration to determine what tool was correct. However, one has to consider that he was also the youngest chimpanzee that we tested. Youngsters represent an interesting case compared to adults because although they may engage more readily than adults in exploration, they may lack the required strength (see "Experiment 2") and/or knowledge about tools to make the required modifications. Also recall that the two orangutans that took longest to discover the use of the cable as a straw were the oldest ones. These individuals represent the opposite case to the young chimpanzee in terms of innovative tendencies and skills—they possessed the strength and the knowledge but they may have been less flexible with regard to innovation. Indeed, the fact that they routinely modified both functional and non-functional tools despite the effort that this represented, especially in the bar task, suggests some degree of inflexibility. Based on these tentative results we can speculate that adolescents and young adults appear to be the best positioned individuals to produce most cases of innovative solutions in complex problem solving tasks. But again, caution is needed when interpreting these results due to our reduced sample size.

Most apes preferentially removed blockages from non-functional tools. More importantly, some orangutans removed blockages prior to using the tool and also identified appropriate tools by just looking at them. This suggests that they could anticipate the effect that blockages had on the flow of juice. Additionally, these data fit well with previous studies that have described apes fashioning tools with certain features prior to their use (McGrew 1992; Sanz et al. 2009). For instance, chimpanzees in the Goulougo triangle in Central Africa manufacture brush-tipped tools by fraying one end of the stick with their teeth. These brushes are prepared prior to inserting the tool in the termite mound and they increase the efficiency of the fishing tool fivefold (Sanz et al. 2009).

Orangutans were able to select the correct of a set of novel tools by just looking at them without having to manually or orally inspect them. This result corroborates a similar finding showing that apes do not need to manipulate a set of novel tools to decide which one is flexible if they can observe an experimenter manipulating them (Manrique et al. 2010). In other words, seeing that some tools bend and others do not provided the apes enough information to allow them to select the correct tool. In the current study, subjects may have chosen the suitable tool by focusing on the presence of openings at the end of the tools that were presented to them. In contrast, subjects failed to use the effects that the tools produced in the environment to decide which tools were suitable to solve the task. In this case, tools were identical but differed in the results that they were associated with. Because orangutans failed Experiment 4 and their success in Experiment 3 could be satisfactorily explained by associative rules, i.e. the subjects learned that some specific tool features (hollowness) correlated with task success; we cannot support our findings by appealing to causal understanding. However, it is true that subjects only witnessed the effects for a brief exposure and that a longer exposure may have produced different results. Additionally, the tools were visually identical which may have made the task harder.

Despite our negative results, future studies should continue to investigate the issue of tool selection based on functional features. Whereas some data have already accumulated on tool selection by primates and birds based on tool length, thickness, weight, size, pliability, and friability (Chappell and Kacelnik 2002, 2004; Mulcahy et al. 2005; Manrique et al. 2010; Tebbich and Bshary 2004; Visalberghi et al. 2009; Bird and Emery 2009), there is very little information on whether individuals can also select suitable tools based on functional properties, more specifically on the effects that tools have on the environment. It remains an open question whether non-human animals would be able to select tools based on observing the effects that the tools have on the environment.

In conclusion, orangutans proved to be more innovative than bonobos and most chimpanzees by inventing the use of tools as straws and modifying non-functional tools when needed. Moreover, some orangutans introduced the required modification prior to using the tools and were able to select novel suitable tools without having to try them first. Although orangutans were able to select tools based on their appearance alone, they were unable to select tools based on the effect that they had on the environment. At a more general level, our study highlights that traditional comparative analyses based on tasks devoid of species-specific propensities are not completely satisfactory as they may underestimate skills (i.e., innovation) based precisely on species-specific propensities. This is not to say that the traditional approach should be completely abandoned, but at the very least, it should be combined with tasks that precisely exploit species-specific propensities. The resulting picture may not be as clear as one based on removing those propensities but at the same time it probably provides a more accurate picture and ecologically valid assessment of the evolution of cognitive abilities.

Acknowledgments Héctor Marín Manrique was supported by a postdoctoral contract funded by the Spanish "Programa de Ayuda a la Movilidad del Ministerio de Ciencia e Innovacion (Micinn)".

References

Beck BB (1980) Animal tool behavior: the use and manufacture of tools by animals. Garland, New York

Bird CD, Emery NJ (2009) Insightful problem solving and creative tool modification by captive non tool-using rooks. Proc Natl Acad Sci USA 106:10370–10375

Chappell J, Kacelnik A (2002) Tool Selectivity in a Non-Primate, the New Caledonian Crow (*Corvus moneduloides*). Anim Cogn 5:71–78

Chappell J, Kacelnik A (2004) Selection of tool diameter by New Caledonian Crows *Corvus moneduloides*. Anim Cogn 7:121–127

Fox EA, Sitompul AF, van Schaik CP (1999) Intelligent tool use in wild Sumatran orangutans. In: Parker ST, Miles HL, Mitchell RW (eds) The mentality of Gorillas and Orangutans. Cambridge University Press, Cambridge, pp 99–116

Girndt A, Meier T, Call J (2008) Task constraints Mask Great Apes' ability to solve the trap-table task. J Exp Psychol Anim Behav Process 34:54–62

Hart BL, Hart LA, McCoy M, Sarath CR (2001) Cognitive behaviour in asian elephants: use and modification of branches for fly switching. Anim Behav 62:839–847

Hunt GR, Gray RD (2004) The crafting of hook tools by wild new Caledonian Crows. Proc R Soc Lon B Suppl 271:S88–S90

Lefebvre L, Whittle P, Lascaris E, Finkelstein A (1997) Feeding innovations and forebrain size in birds. Anim Behav 53:549–560

Manrique HM, Gross A, Call J (2010) Great apes select tools on the basis of their rigidity. J Exp Psychol Anim Behav Process 36(4):409–422

Martin-Ordas G, Call J (2009) Assessing generalization within and between trap tasks in the great apes. Int J Comp Psychol 22:43–60

Martin-Ordas G, Call J, Colmenares F (2008) Tubes, tables and traps: great apes solve two functionally equivalent trap tasks but show no evidence of transfer across tasks. Anim Cogn 11:423–430

McGrew WC (1992) Chimpanzee material culture: implications for human evolution. Cambridge University Press, Cambridge

Mendes N, Hanus D, Call J (2007) Raising the level: orangutans use water as a tool. Biol Lett 3:453–455

Mulcahy NJ, Call J (2006a) Apes save tools for future use. Science 312:1038–1040

Mulcahy NJ, Call J (2006b) How great apes perform on a modified trap-tube task. Anim Cogn 9:193–199

Mulcahy NJ, Call J, Dunbar RIM (2005) Gorillas (*Gorilla gorilla*) and Orangutans (*Pongo pygmaeus*) Encode Relevant Problem Features in a Tool-Using Task. J Comp Psychol 119:23–32

O'Malley RC, McGrew WC (2000) Oral tool use by captive orangutans (*Pongo pygmaeus*). Folia Primatol 71:334–341

Osvath M, Osvath H (2008) Chimpanzee (*Pan troglodytes*) and orangutan (*Pongo abelii*) forethought: self-control and pre-experience in the face of future tool use. Anim Cogn 11:661–674

Reader SM, Laland KM (2002) Social intelligence, innovation and enhanced brain size in primates. Proc Natl Acad Sci USA 99:4436–4441

Sanz C, Call J, Morgan D (2009) Design complexity in termite-fishing tools of chimpanzees (*Pan troglodytes*). Biol Lett 5:293–296

Sol D, Timmermans S, Lefebvre L (2002) Behavioural flexibility and invasion success in birds. Anim Behav 63:495–502

Tebbich S, Bshary R (2004) Cognitive abilities related to tool use in the Woodpecker Finch, *Cactospiza pallida*. Anim Behav 67:689–697

Tomasello M, Call J (1997) Primate cognition. Oxford University Press, New York

van Schaik CP, Knott CD (2001) Geographic variation in tool use on *Neesia* fruits in orangutans. Am J Phys Anthrop 114:331–342

Visalberghi E, Addessi E, Truppa V, Spagnoletti N, Ottoni E, Izar P, Fragaszy D (2009) Selection of effective stone tools by wild bearded capuchin monkeys. Curr Biol 19:213–217