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ORIGINAL PAPER

Understanding the functional properties of tools: chimpanzees (*Pan troglodytes*) and capuchin monkeys (*Cebus apella*) attend to tool features differently

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Abstract We examined whether eight capuchins and eight chimpanzees were able to retrieve a reward placed inside a tube, of varying length, by selecting the correct stick from different sets of three sticks differing in length (functional feature) and handle (non-functional feature). Moreover, to investigate whether seeing the stick inside the tube (visual feedback) improves performance, half of the subjects were tested with a transparent apparatus and the other half with an opaque apparatus. Phase 1 included (a) Training 1 in which each stick had a different handle and (b) Transfer 1 in which the handles were switched among sticks, so that the functional tool had the same length but a different handle than before. The seven chimpanzees and one capuchin that passed Transfer 1 received Transfer 2. The other subjects received (a) Training 2, which used the same sticks from Phase 1 with handles switched in every trial, and (b) Transfer 2 in which the tube was longer, all sticks had the same new handle, and the formerly longest tool became intermediate in length. Eight chimpanzees and three capuchins passed Transfer 2. Results showed that (1) chimpanzees applied relational structures in tool using tasks more quickly than capuchins and (2) capuchins required more varied experience to attend to the functional feature of the tool. Interestingly, visual feedback did not improve performance in either species.

Keywords Tool use · Functional features · Relational rules · Visual feedback · Primates

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Introduction

Relational representations involve encoding the properties of objects in relation to other objects (Call 2000). Tool use is a classic example, since the actor establishes a relationship between an object (the tool) and other object(s) and/or surface(s) by producing specific actions in order to achieve a goal (Visalberghi and Fragaszy 2006). Although several animal species use tools in a variety of contexts (Shumaker et al. 2011), it is still unclear whether or not they have a similar appreciation of the necessary characteristics that objects should have to be functional (e.g. Bluff et al. 2007; Holzhaider et al. 2008; Povinelli 2000; Santos et al. 2006; Visalberghi and Limongelli 1996).

Investigating animals' ability to select the functional tool among various objects with different features and then use the selected tool to achieve the desired goal has a long tradition in comparative psychology (Köhler 1925/1976; Klüver 1933; for reviews see also Fragaszy et al. 2004, chapters 9 and 10; and Tomasello and Call 1997, chapter 3). Both in captivity and in the wild, chimpanzees and capuchin monkeys treat functional and non-functional tool features differently and flexibly adapt to the requirements of the task at hand (e.g. Boesch and Boesch 1990; Manrique et al. 2010; Manrique et al. 2011; McGrew 1992; Visalberghi et al. 2009; Whiten et al. 1999). For example, chimpanzees (captivity: Nash, 1982; Lonsdorf et al. 2009; Paquette, 1992; wild: Goodall 1986, chapter 18; Bermejo and Illera 1999; Sanz et al. 2009) and capuchins (captivity: Fragaszy et al. 2004, chapter 10; wild: Mannu and Ottoni 2009; Souto et al. 2011) extract food with probing sticks. However, the extent to which the tools selected possess the appropriate length to reach the goal has seldom been considered in captive studies (e.g. Anderson and Henneman 1994; Chappell and Kacelnik 2004; Mulcahy et al. 2005) and is difficult to study in the wild, since the targeted food items are frequently at unknown depths inside the natural substrates (e.g. termite mounds, tree trunks).

Two paradigms, both involving a horizontal transparent tube task, have been used to investigate whether the length of a tool is taken into consideration when solving a problem. The first paradigm requires selection among tool sticks of different lengths. When presented with a transparent horizontal tube, baited at different distances from the opening, and sticks of different lengths, New Caledonian crows (Chappell and Kacelnik 2002) generally selected sticks whose length matched the distance between the reward and the opening of the tube. In contrast, woodpecker finches (Tebbich and Bshary 2004) and human adults (Silva and Silva 2010) selected longer sticks, though not necessarily the longest stick of the set.

The second paradigm requires the combination or modification of potential tools. Capuchins were presented with tools that were too thick (sticks taped together forming a bundle too wide to fit in the tube), too short (three short sticks that together equalled the length required), or blocked (a stick with thin sloping wooden blocks on either end). Subjects solved these conditions by dismantling the bundle, inserting one stick after the other, and removing the blocking pieces, respectively. While solving the tube task, they continued to make errors suggesting a poor comprehension of the necessary length of the stick to displace the reward (Visalberghi and Trinca 1989; Visalberghi et al. 1995). Apes and children performed better than capuchins, as their error rates decreased across trials (Troise 1991; Visalberghi et al. 1995), suggesting a quicker appreciation of the role of length.

Both paradigms have mostly used transparent tubes, on the assumption that visual access, of the production of reward movement by the stick, is valuable for species relying on vision, as in primates and birds. A transparent tube allows the subject to perceive the effect of its own action on the reward and acquire a proper knowledge of the relationship between action and outcome. In contrast, an opaque tube prevents this, thus favouring associative learning as the main mechanism responsible for the solution. Chimpanzees and children find the solution to a problem faster when they can observe how it works, compared to situations in which the only available information is an arbitrary regularity (Hanus and Call 2008; Hanus and Call 2011; Seed and Call 2009). However, this hypothesis still needs to be tested in the case of the horizontal tube task.

In the present study, we used a modified version of the first paradigm with capuchins and chimpanzees. Our first goal was to assess whether and how having experience with a tool task gave subjects an appreciation of the features that make objects effective as tools. For this, we used different sets of tools consisting of sticks of different lengths (functional feature) and handles, of differing shape and colour (non-functional feature). Our second goal was to evaluate whether the path to the solution and success rate were affected by the information subjects may acquire by having visual access of the functioning of the apparatus. To this purpose, the same apparatus was used in a transparent condition and an opaque condition.

Both capuchin monkeys and chimpanzees transfer relationships from one situation to a different one (capuchins: Spinozzi et al. 2004; Truppa et al. 2010, 2011; chimpanzees: Flemming et al. 2008; Haun and Call 2009; Hribar et al. 2011; Thompson et al. 1997). Kennedy and Fragaszy (2008) investigated whether four capuchins could match cups from two sets based on their common relative size within the set. Specifically, the subject was required to find a reward in his set of cups after observing another reward being hidden in an experimenter's set. One capuchin successfully chose the cup in his set that was the same relative size as the baited cup in the experimenter's set. Chimpanzees tested with the same relative-size-matching task required roughly four times fewer trials than did capuchins (Flemming and Kennedy 2011). Importantly, neither species chose the cup of the same absolute size as the experimenter's baited cup over the cup of the same relative size. The third goal of our experiment was to investigate whether subjects in Phase 1 who chose the longest tool will in Phase 2 continue to choose the stick of the same relative length (i.e. the longest stick) or will they choose the stick of the same absolute length (i.e. the stick that was the longest in Phase 1 but the medium one in Phase 2).

Since both species learn to use functional features of the tools to inform their tool selection and relational learning processes are faster in chimpanzees than in capuchins, we predict that (1) both species will learn that the length is the functional property of the tool; (2) visual access will improve performance; and (3) both species will select tools on the basis of a relational rule and that chimpanzees will be faster than capuchins at acquiring it.

Methods

Subjects

Capuchins

We tested 8 adult tufted capuchin monkeys (*Cebus apella*, four males and four females ranging from 8 to 30 years of age) hosted at the Primate Centre of the Institute of Cognitive Sciences and Technologies (see Table 1 for details). The monkeys live in two groups (group A, $N = 5$ and group B, $N = 6$), each housed in an indoor–outdoor enclosure. Both groups have two indoor cages separated by a concrete wall (each 2.5 m^2 $\times$ 2.75 m high) and connected through a sliding door, and one outdoor enclosure (group A: 40 m^2 $\times$ 3 m high; group B: 48 m^2 $\times$ 3 m high). Capuchins were tested individually in the indoor cages, which they have access to through sliding doors connected to the outdoor enclosure. Each subject was separated from the group for testing just before the daily session. Water was freely available at all times, and food (monkey chow, Altromin-A pellets, Rieper standard diet for primates, and fresh fruits and vegetables) was provided in the afternoon after testing. Tests were conducted between June 2008 and February 2009. All subjects had participated in other studies concerning cognitive and perceptual abilities. Furthermore, many years before, the six older capuchins had had repeated experience with tools and the transparent horizontal tube (studies in which they were not required to select always the longest/biggest tool/object; Visalberghi and Limongelli 1994; Visalberghi and Trinca 1989; Visalberghi unpublished results). In contrast, the two younger ones had not and were familiarized with the tube task at the beginning of this study.

Chimpanzees

We tested adolescent and adult chimpanzees (*Pan troglodytes*), five females and three males ranging from 8 to 16 years of age, hosted at the Wolfgang Köhler Primate Research Centre in the Leipzig Zoo (see Table 1 for details). They are housed in two social groups: group A consisted of 19 individuals and group B of 6 individuals. The housing facilities consist of large outdoor and indoor compounds, sleeping rooms, and observation rooms. The compounds and indoor rooms are connected to each other by passageways. Chimpanzees were tested individually either in a sleeping room or in an observation room. Chimpanzees were fed several times a day, and water was available ad libitum. Tests were conducted between March and May 2009. All chimpanzees had previously participated in a number of cognitive studies, some of which also required them to use tools; however, only five of them had had some experience with a trap-tube task (Mulcahy and Call 2006; Martin-Ordas et al. 2008; Martin-Ordas and Call 2009; Seed et al. 2009), and none of them had participated in any study that would require them to select the longest/biggest tool/object. The other three subjects were familiarized with the tube task at the beginning of this study.

Apparatus and tools

Capuchins

The apparatus consisted of a Plexiglas box (40 cm long $\times$ 40 cm high $\times$ 15 cm wide; see Fig. 1) containing a transparent tube (20 or 25 cm long with inner diameter of 1.9 cm) fixed on a horizontal platform that the subject could access with a stick tool. The experimenter baited the tube in full view of the subject. Specifically, (s)he placed the reward (a peanut kernel) in the tube's farthest point from the subject's point of view. The tool had to be long enough to push the reward down onto an inclined plane, which led to an opening at the bottom of the box where the subject could pick it up. There were two experimental conditions: (1) in the transparent condition, all the parts described above were in view; and (2) in the opaque condition, the Plexiglas box was covered by an opaque wooden panel so that the subject could not observe the effect of her/his stick inserted in the tube (since the tool obstructed it when inserted). Furthermore, monocular viewing into the relative dark interior of the tube did not allow subjects to assess how far the reward was from the entrance. The only information that could be acquired was whether the tube was rewarded or not (Sabbatini, personal observations). Each tool consisted of a stick with a handle attached to one of its sides. Four sets of three different tools were used. The tools (diameter 1.3 cm) differed in length and handle shape and colour (Fig. 2a). The length of the sticks was such that in each set, only the longest tool could reach the reward. The tools were presented upright in a Plexiglas choice box at 10 cm distance from one another so that both the length and the handle of each tool were in full view to the subject (Fig. 2). The choice box was placed outside the cage, at the wire-mesh wall, and the subject could choose among the three tools by inserting her/his finger in one of the 1.3-cm holes positioned in front of each tool (see Fig. 3a). The experimenter then retrieved the choice box and gave the chosen tool to the subject.

Chimpanzees

The apparatus and conditions were similar to those described for capuchins with a few minor differences (see Fig. 3b). Tools (sticks and handles) were more robust but looked almost identical to those used with capuchins. The

Table 1 Demographics of subjects and their previous success or failure (F) with tool using tube tasks

	Group	Sex	Age (in years)	Rearing	Previous experience
Capuchin monkey's name					
Cammello	A	M	30	Hand	1
Carlotta	A	F	24	Hand	1, 3^{F}
Gal	A	M	18	Hand	2
Paprica	A	F	19	Hand	2
Pippi	B	F	27	Hand	1, 3^{F}
Roberta	B	F	22	Hand	3
Sandokan	B	M	8	Hand	
Vispo	B	M	8	Mother	
Chimpanzee's name					
Fifi	B	F	16	Mother	4, 5, 6
Jahaga	B	F	16	Mother	5^{F}
Alex	B	M	8	Nursery	
Alexandra	B	F	10	Nursery	
Annett	B	F	10	Nursery	
Sandra	A	F	16	Mother	5, 6, 7
Lome	A	M	8	Mother	7
Patrick	A	M	12	Mother	7^{F}

(1), Visalberghi and Trinca (1989); (2), Visalberghi, unpublished results; (3), Visalberghi and Limongelli (1994); 3^{F}, subject failed in this task; (4), Mulcahy and Call (2006); (5), Martin-Ordas et al. (2008); 5^{F}, subject failed in this task; (6), Martin-Ordas and Call (2009); (7), Seed et al. (2009); 7^{F}, subject failed in this task

Fig. 1 An adult female capuchin has inserted the long tool inside the transparent tube fixed on a horizontal platform placed inside the apparatus. The tool is long enough to reach and displace the reward (a peanut placed on the tube farther side from the subject's point of view), so that by dropping onto an inclined plane it falls in an opening at the *bottom* of the *box* where the subject can pick it up. Photograph by Elisabetta Visalberghi

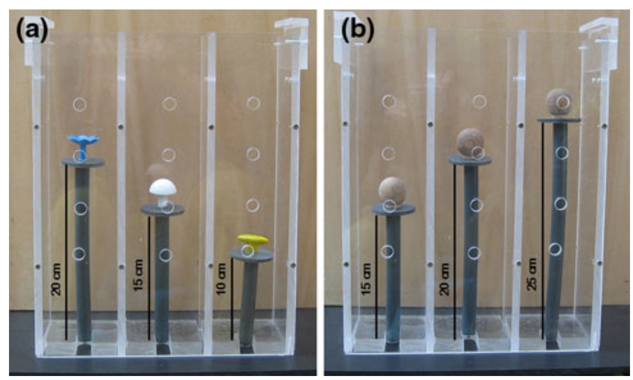

Fig. 2 Examples of tools employed in Phase 1 and training of Phase 2 (**a**) and in transfer of Phase 2 (**b**). Each set of tools consisted of 3 *grey sticks* differing in terms of length and handle shape and colour. In **a**, the 10-cm stick has the *yellow handle*, the 15-cm stick has the *white handle*, and the 20-cm stick has the *blue handle*. In **b**, all three sticks have the same handle (a *round brown ball*) but different lengths: short (15 cm), medium (20 cm), and long (25 cm). The tools are presented upright on a Plexiglas choice box, and the subject could choose among the three tools by inserting her/his finger in one of the holes positioned in front of each tool (colour figure online)

apparatus was positioned on a table outside of the cage and in contact with a wire-mesh panel. Since the cages were already furnished with a Plexiglas panel (70 cm × 50 cm), the tools were attached vertically to a sliding table (80 cm × 35 cm). The Plexiglas panel had three 5-cm holes, with a distance of 30 cm between them, through which the chimpanzee could insert a finger to indicate her/his choice. Each tool was placed in front of a hole with a 30-cm distance between the tools.

Procedure

The experiment consisted of one familiarization phase followed by two experimental phases. To investigate whether seeing the consequences of the tool movements inside the tube (i.e. visual feedback) improved performance, half of the subjects (for both capuchins and chimpanzees) were tested with a transparent apparatus

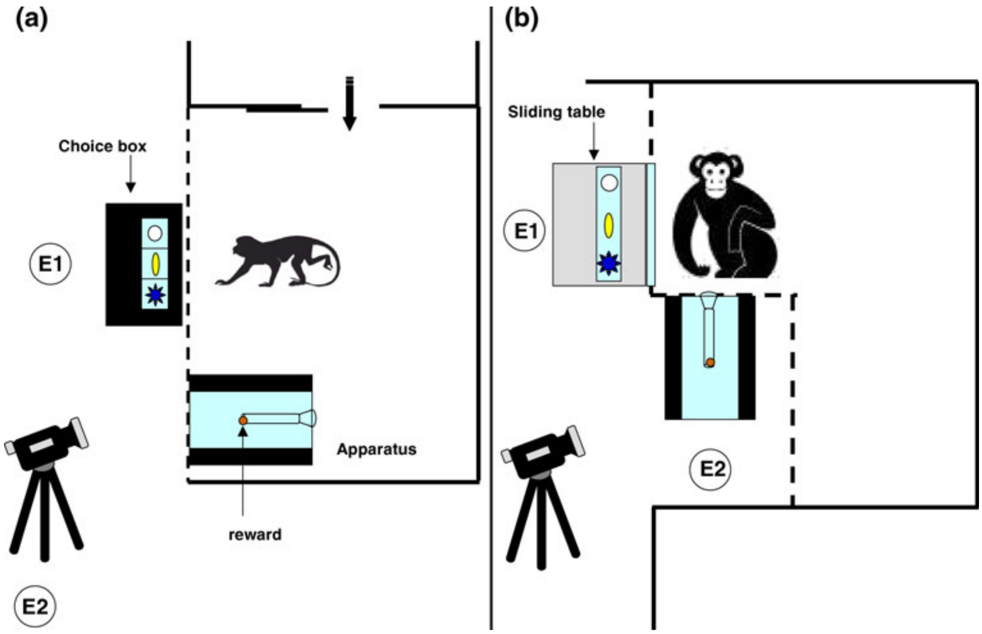

Fig. 3 Bird's-eye view of the experimental set-up adopted for capuchins (**a**) and for chimpanzees (**b**). E1 positions the three tools inside the choice box out of the subject view, and then the capuchin subject is allowed to enter in the experimental cage and to choose among the three tools (**a**) or on the sliding table behind an opaque panel and then the chimpanzee subject is allowed to choose among the three tools (**b**). Then, E1 hands the chosen tool to the subject that can use it with the apparatus inside the cage (**a**) or attached to the wire-mesh outside the cage (**b**). After insertion with the tool, capuchin subject is moved to the adjacent cage so that the experimenters could retrieve the tool (**a**), while the chimpanzee subject is asked to return the tool (**b**). The experimental sessions are videotaped

(transparent condition) and the other half with an opaque apparatus (opaque condition; see above for details).

Familiarization phase

The aim of this phase was to familiarize each subject with the first set of tools. The familiarization phase was slightly different for capuchins and chimpanzees because the latter had previously been trained to give back their tools to the experimenter and capuchins had not. In the case of capuchins, the experimenter (E) placed the baited apparatus and all three tools inside the testing cage and then let the subject enter so that (s)he had the opportunity to manipulate them. Each subject experienced at least five insertions with each tool; only the insertion of the longest one allowed the retrieval of the reward. After five insertions with one tool, E removed it and left the other tools inside the cage; after five insertions with the second tool, E removed it and left the last tool inside the cage until the fifth insertion. In the case of chimpanzees, the subject was first given the shortest tool. After at least one insertion, the subject was asked to give back the short tool and received the middle tool. After at least one insertion of the middle tool, the subject was asked to give it back and received the long tool (i.e. the functional tool). The subject's insertion of the tool allowed retrieval of the reward, and the subject was asked to give the tool back.

Experimental phases

There were two experimental phases, each consisting of a training period and a transfer test. In these phases, there were two experimenters (E1 and E2) with different roles. The procedure was the same throughout the experiment, for the training and transfer test, for both phases and almost identical for the capuchin monkeys and chimpanzees. At the beginning of each trial, E2 placed the reward inside the tube unless the reward from previous unsuccessful trial(s) was already there. E1 positioned the three tools inside the choice box (for the capuchins) or on the table (for the chimpanzees) out of the subject's view. Then, the capuchins were allowed to enter the experimental cage, whereas the chimpanzees stayed in the same cage throughout the session. Next, the subject was offered a choice among three tools, two non-functional tools and one functional tool (see below). E1 gave them the chosen tool, and the subject then tried to obtain the reward with that tool. After success with the functional tool or one or more insertions with the non-functional tool, the capuchin was sent to the adjacent cage, so that E2 could retrieve the tool and rebait the apparatus; the chimpanzees were asked to return the tool (for examples of the procedure with chimpanzees, see Videos 1 and 2 in the supplementary material). The positions of the three tools were randomized and counterbalanced across trials so that each tool was presented six times in each position (right, middle, left) and could be in the same position for no more than two consecutive trials. Trials lasted until recovery of the reward or until 1 min had elapsed. The two phases differed in the types of tools subjects were given and in the length of the tube. The reward was always positioned at the end of the tube; according to the length of the tube, the reward was at a distance of 19 or 24 cm from the opening. In both phases, each session included 18 trials. When a subject met the criterion of at least 12 out of 18 correct choices for 2 consecutive sessions, the transfer test started. In both transfers, each subject received a total of 36 trials during two 18-trial-daily sessions.

Phase 1. In Training 1, the presented set consisted of three tools: a 10-cm stick with a blue handle (short–blue tool), a 15-cm stick with a yellow handle (medium–yellow tool), and a 20-cm stick with a white handle (long–white tool). Only the longest tool was functional. After the subject met the criterion, (s)he went on to Transfer 1 where (s)he was presented three very similar but different tools: a 10-cm stick with a white handle (short–white tool), a 15-cm stick with a blue handle (middle–blue tool), and a 20-cm stick with a yellow handle (long–yellow tool). The handles were switched among tools so that the functional tool had the same length as in the training but a different handle. The goal of the transfer test was to evaluate which characteristic of the tool the subjects paid attention to when they picked the effective tool in the training. If the subject used length (as opposed to the handle) as the relevant feature, (s)he will choose the longest stick again and not the white handle. We expected those subjects that had learned to select the tool based on the functional feature (i.e. length) to pass the transfer and subjects that learned to select the tool on the basis of the non-functional feature (i.e. handle) to fail the transfer. If the subject succeeded in the transfer test, (s)he proceeded directly to the transfer of Phase 2; otherwise, (s)he proceeded to the training of Phase 2.

Phase 2. In Training 2, nine different tools were used; sticks could be three different lengths (short 10 cm, medium 15 cm, or long 20 cm), and each length could have any of the three handles (blue, yellow, or white) on it. The functional tool was always the long one, but the appearance of its handle changed with every trial. Again, when subjects reached the criterion, they continued with Transfer 2 where a new set of three different tools was used. All three of them had a new identical handle (a round brown ball) and were three different lengths: short (15 cm), medium (20 cm), and long (25 cm) (Fig. 2b). Thus, the length that was the longest (and the correct one) during the training phase (20 cm) became the medium one in the transfer. Since the baited tube was longer in the transfer than in the training, the reward could only be obtained by using the longest (25 cm) of the three tools provided; success in the transfer required selecting the longest stick and not the stick whose absolute length was previously rewarded.

Coding and statistical analyses

The experimental phases were videotaped, and the behaviours were scored live and from tapes. The variables scored in each trial were tool selected and success. In both phases, training lasted until a criterion of at least 12 correct responses, out of 18 trials, in two consecutive sessions (binomial test: $\alpha < 0.01$). Transfer tests consisted of two 18-trial sessions. The transfer was considered successfully completed when subjects performed 12 or more correct trials, out of 18, in each session (binomial test: $\alpha < 0.01$). To assess whether the number of trials needed to reach criterion during training and the number of functional tool choices selected during transfer differed between capuchin monkeys and chimpanzees, we carried out a Mann–Whitney U test. To evaluate condition effect (opaque vs. transparent) in the number of trials needed to reach criterion during the training and in the number of functional tool choices selected during the transfer, we carried out a Mann–Whitney U test. To test whether there was a species difference between correct and incorrect responses in Trial 1 of the transfers, we carried out a Fisher's exact test. To assess whether the percentage of choice differed between pairs of handles or sticks (white–yellow, white–blue, yellow–blue or long–medium, long–short, medium–short), we carried out Wilcoxon's matched-pairs tests. Since two comparisons were made, we applied Bonferroni's correction, with the corrected alpha level (α^*) set at 0.02. The number of correct choices between the two sessions of each transfer was compared with a Wilcoxon's matched-pairs test. Statistical tests were typically two-tailed (exceptions are noted as they occurred). Descriptive statistics include the median and the interquartile range (IQR).

Results

Table 2 provides descriptive information on each subject's individual performance.

Phase 1: Training 1

Capuchins needed significantly more trials than chimpanzees to reach criterion in Training 1 (Mann–Whitney test: $U = 7$, $P < 0.01$; with median = 81, IQR = 63 and median = 54, IQR = 18, respectively). We found no statistical difference between the opaque and transparent conditions in the number of trials needed to reach criterion for either species (Mann–Whitney test: capuchins, $U = 8$, $P = 1$; chimpanzees, $U = 7.5$, $P = 0.88$; Fig. 4).

Table 2 Summary of capuchins' and chimpanzees' results

	Condition	No. of training sessions to criterion		% Correct on the (last) two sessions			
				Phase 1		Phase 2	
		Phase 1	Phase 2	Training	Transfer	Training	Transfer
Capuchin subject							
Cammello	Opaque	8	18	92	0	67	61
Paprica	Opaque	4	15	78	6	78	78
Pippi	Opaque	5	10	92	14	78	53
Sandokan	Opaque	4	7	92	17	83	44
Carlotta	Transparent	7	10	89	17	69	50
Gal	Transparent	3	/	67	97[a]	/	36
Roberta	Transparent	9	6	86	8	69	81
Vispo	Transparent	4	8	100	39	81	86
Mean		6	10	86	25	75	64
Chimpanzee subject							
Patrick	Opaque	6	/	72	81	/	69
Alexandra	Opaque	2	/	83	92	/	89
Annett	Opaque	3	/	100	92	/	86
Jahaga	Opaque	2	/	86	100	/	78
Fifi	Transparent	3	/	92	92	/	100
Sandra	Transparent	2	2	83	56[b]	78	72
Lome	Transparent	3	/	86	92	/	78
Alex	Transparent	3	/	86	94	/	75
Mean		3	2	86	87	78	81

[a] Gal reached the criterion for Phase 1 transfer

[b] Sandra did not reach the criterion for Phase 1 transfer

No species difference was found in the numbers of correct and incorrect responses in Trial 1 (Fisher's exact test: $P = 0.57$). Neither capuchins nor chimpanzees showed a preference towards the longest tool on the first trial of this training (one-tailed binomial tests: $P = 0.20$ and $P = 0.52$, respectively). Capuchins reached criterion between sessions 3 and 9 (Fig. 4a, b). During training, capuchins selected the long–white tool significantly more often than the medium–yellow or the short–blue tools (Wilcoxon's test: $T = 0$, $P = 0.01$ and $T = 0$, $P = 0.01$, respectively). Moreover, there was no significant difference in the number of times the medium–yellow and short–blue tools were chosen (Wilcoxon's test: $T = 6$, $P = 0.09$). Chimpanzees reached criterion between sessions 2 and 6 (Fig. 4c, d). During training, chimpanzees selected the long–white tool significantly more often than the medium–yellow (Wilcoxon's test: $T = 0$, $P = 0.01$) or the short–blue tool (Wilcoxon's test: $T = 0$, $P = 0.01$). They also preferred the medium–yellow over the short–blue tool (Wilcoxon's test: $T = 0$, $P = 0.01$).

Phase 1: Transfer 1

Capuchins' percentage of correct trials was significantly lower than chimpanzees' in the transfer test of Phase 1 (Mann–Whitney test: $U = 7$, $P < 0.01$, with median = 15.3, IQR = 20.8, and median = 91.7, IQR = 6.9, respectively). Moreover, no statistical difference, between the opaque and transparent conditions, in the percentage of functional tool choices in the two conditions for the two species was found (Mann–Whitney test: capuchins, $U = 2.5$, $P = 0.11$; chimpanzees, $U = 7$, $P = 0.88$; Fig. 5). No species difference was found in the numbers of correct and incorrect responses in Trial 1 (Fisher's exact test: $P = 0.31$).

In the transfer test, only one capuchin monkey (Gal), belonging to the transparent condition, succeeded (Fig. 5a). Capuchins did not choose the longest tool above chance level on Trial 1 (one-tailed binomial test: $P = 0.52$). Capuchins selected the long–yellow and the short–white tools significantly more than the medium–blue tool (Wilcoxon's test: $T = 0$, $P < 0.02$ and $T = 0$, $P < 0.02$, respectively). Note that the order of their handle preferences (yellow = white > blue) closely resembles that of Training 1. Moreover, there was no significant difference between the number of times in which the long–yellow and short–white tools were selected (Wilcoxon's test: $T = 7$, $P = 0.12$). There was no significant improvement between the two sessions (Wilcoxon's test: $T = 8.5$, $P = 0.35$). All but one of the chimpanzees succeeded in this transfer test

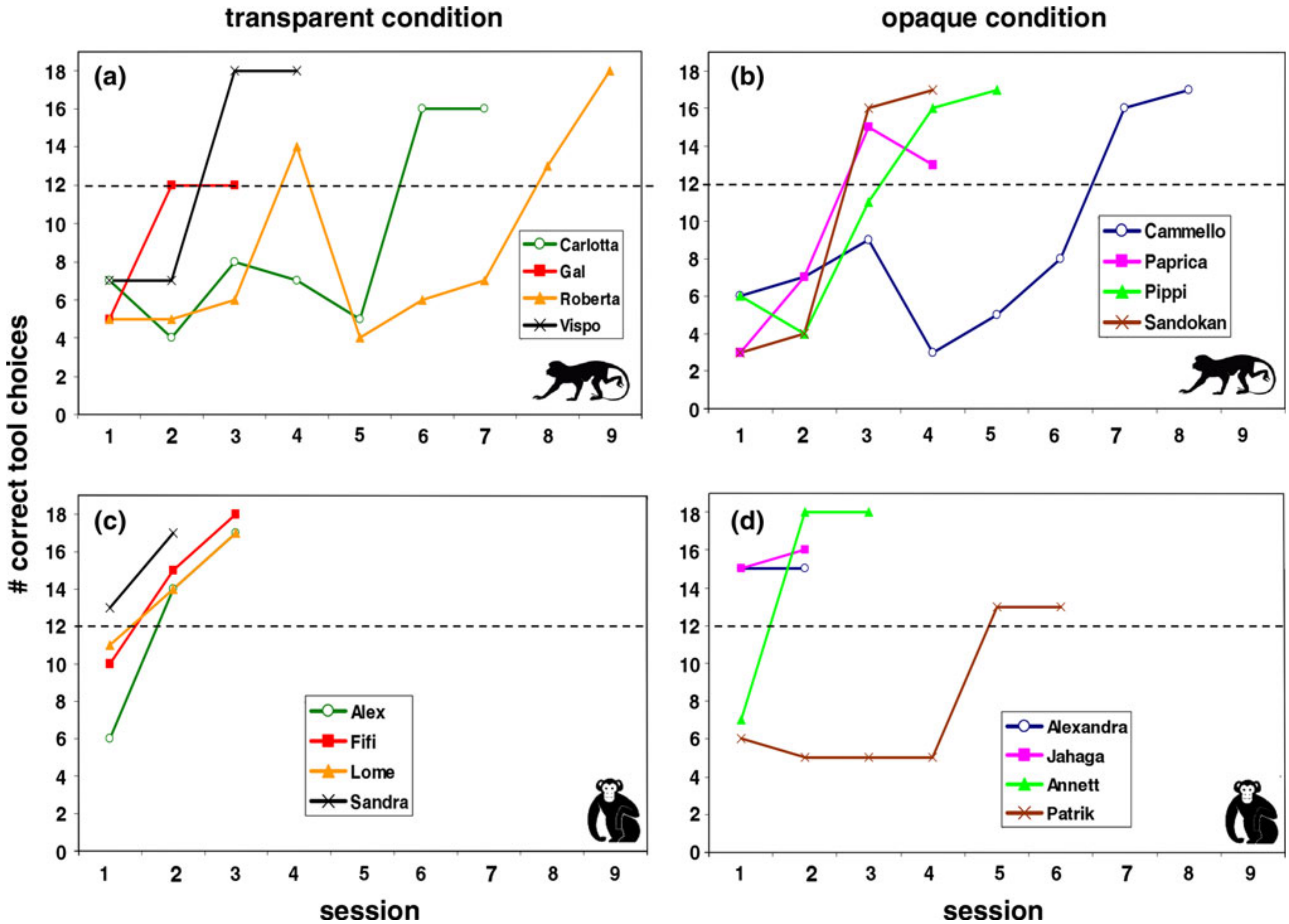

Fig. 4 Number of correct trials across 18-trial sessions in training of Phase 1 for capuchins (**a**, **b**) and chimpanzees (**c**, **d**) in transparent and opaque conditions. The *dotted lines* represent significance levels

(Fig. 5c, d). Chimpanzees chose the longest tool above chance in Trial 1 (one-tailed binomial test: $P = 0.02$). Chimpanzees chose the long–yellow tool significantly more often than the medium–blue (Wilcoxon's test: $T = 0$, $P < 0.02$) or the short–white tools (Wilcoxon's test: $T = 0$, $P < 0.02$). They also chose the medium more often than the shortest tool (Wilcoxon's test: $T = 0$, $P < 0.02$). There was no significant improvement between the two sessions (Wilcoxon's test: $T = 8.5$, $P = 0.35$).

Phase 2: Training 2

During this training, in which length–handle relationship was systematically varied across trials, there was no statistical difference between opaque and transparent conditions, for capuchins, in the number of trials needed to reach criterion (Mann–Whitney test: $U = 2.5$, $P = 0.23$, with median = 180, IQR = 144; Fig. 6). Capuchins reached criterion between sessions 6 and 18 (see Fig. 6a, b). During training, capuchins selected the yellow and the white handles significantly more often than the blue handle (Wilcoxon's test: $T = 0$, $P < 0.02$ and $T = 0$, $P < 0.02$, respectively). There was no significant difference in the number of times that the yellow and white handles were selected (Wilcoxon's test: $T = 6$, $P = 0.18$). Sandra, the only chimpanzee that needed training in Phase 2, reached the criterion in the second session of training (Fig. 6c). She chose each handle a similar number of times (white = 28 %; yellow = 44 %; blue = 28 %).

Phase 2: Transfer 2

In this transfer, in which all sticks had the same new handle and the baited tube was longer than before**,** chimpanzees performed better than capuchins, though this trend falls short of significance (Mann–Whitney test: $U = 14.5$, $P = 0.06$, with median = 56.9, IQR = 31.9 and median = 77.8, IQR = 13.9, respectively). Moreover, no statistical difference was found, between the opaque and transparent conditions, in the percentage of functional tool

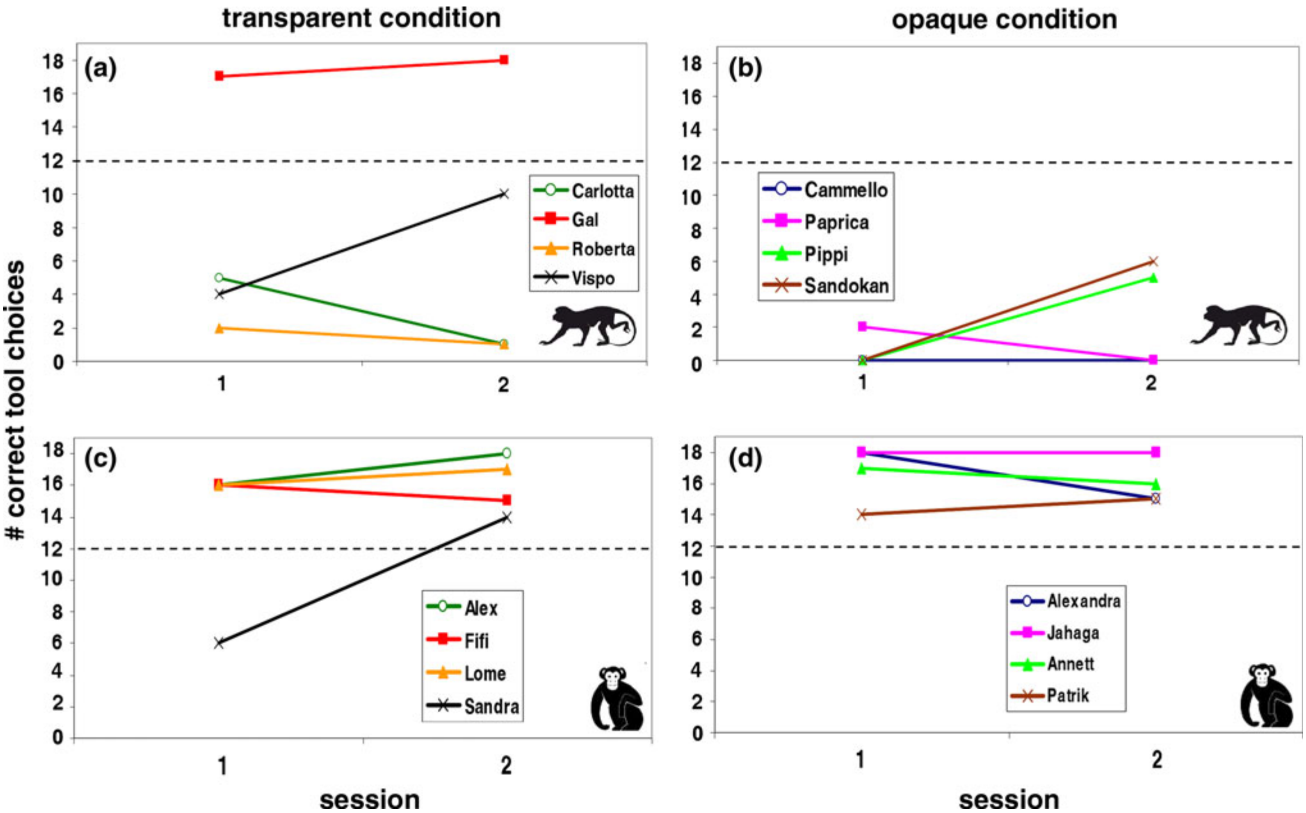

Fig. 5 Number of correct trials across 18-trial sessions in transfer of Phase 1 for capuchins (**a**, **b**) and chimpanzees (**c**, **d**) in transparent and opaque conditions. The *dotted lines* represent significance levels

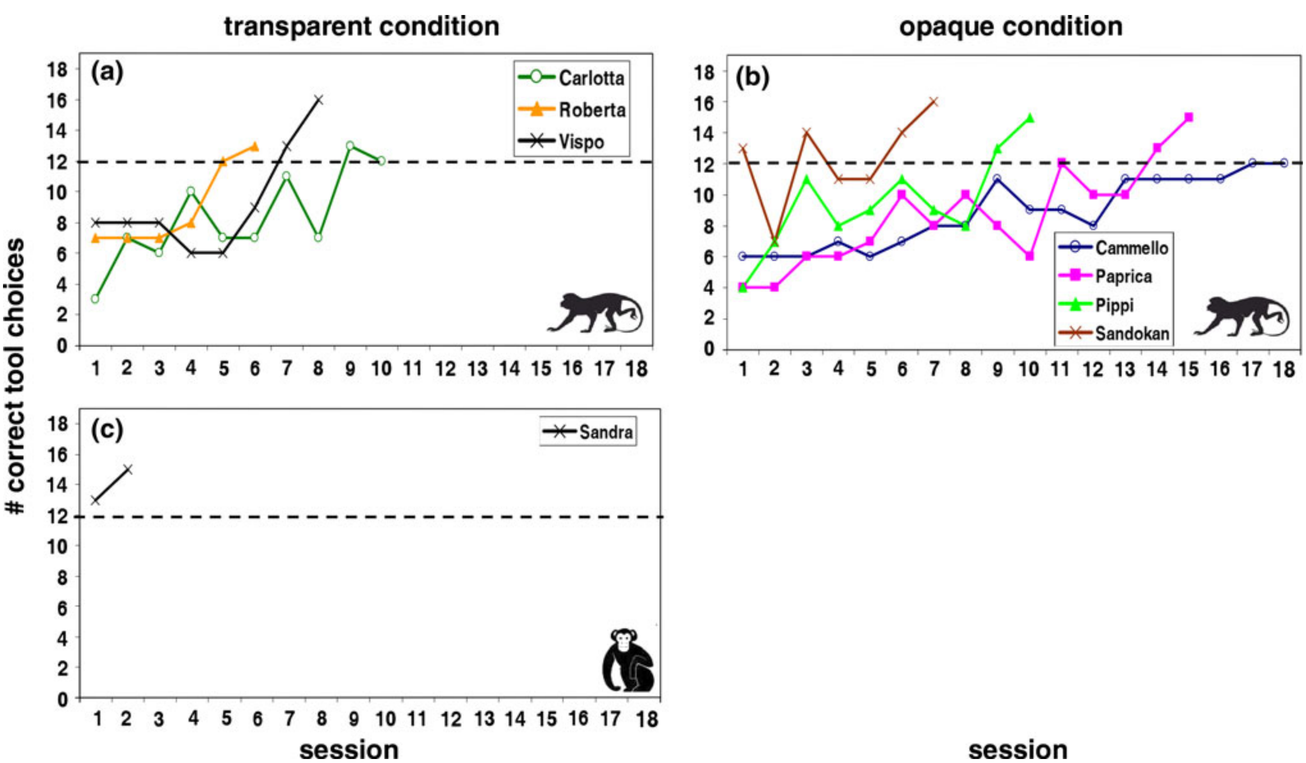

Fig. 6 Number of correct trials across 18-trial sessions in training of Phase 2 for capuchins (**a**, **b**) and the chimpanzee Sandra (**c**) in transparent and opaque conditions. The *dotted lines* represent significance levels

choices, in the two conditions for the two species (Mann–Whitney test: capuchins, $U = 7$, $P = 0.88$; chimpanzees, $U = 7.5$, $P = 0.88$; Fig. 7). No species difference was found in the numbers of correct and incorrect responses in Trial 1 (Fisher's exact test: $P = 0.31$).

Three out of eight capuchins (one subject from opaque condition and two subjects from the transparent condition) passed the transfer (Fig. 7a, b). Gal, the subject that succeeded in the previous transfer, failed in this second transfer. Capuchins did not choose the longest tool above chance in Trial 1 (one-tailed binomial test: $P = 0.52$). Capuchins selected the long tool significantly more often than the medium ($T = 1$, $P = 0.01$) or short tools ($T = 0$, $P = 0.01$) and selected the medium tool more than the short tool ($T = 1$, $P = 0.01$). There was no significant improvement between the two sessions (Wilcoxon's test: $T = 6.5$, $P = 0.20$). All chimpanzees passed Transfer 2, which means they all chose the longest tool in both sessions 12 times or more (Fig. 7c, d). Chimpanzees chose the longest tool above chance in Trial 1 (one-tailed binomial test: $P = 0.02$). Chimpanzees chose the longest tool significantly more often than the medium or shortest tools (Wilcoxon's test: $T = 0$, $P = 0.01$, in both cases). They also chose the medium more often than the shortest tool (Wilcoxon's test: $T = 0$, $P = 0.01$). There was no significant improvement between the two sessions (Wilcoxon's test: $T = 12.5$, $P = 0.79$).

Discussion

Most capuchins, when provided with fixed associations between stick length and stick handle (Phase 1), selected the tools on the basis of the non-functional feature (i.e. shape and colour of the handle). However, all capuchins learned to attend to the functional feature when provided with variable associations between stick length and stick handle (Phase 2). Chimpanzees, on the other hand, already attended to the functional feature in Phase 1. Therefore, the results support our first prediction; both species were able to attend to the functional property of the tool. Our second prediction, which stated that both capuchins and chimpanzees would perform better when they had visual access to the tube, was not supported by the results. Subjects from both conditions, transparent and opaque, performed equally well. Lastly, all chimpanzees and three capuchins passed

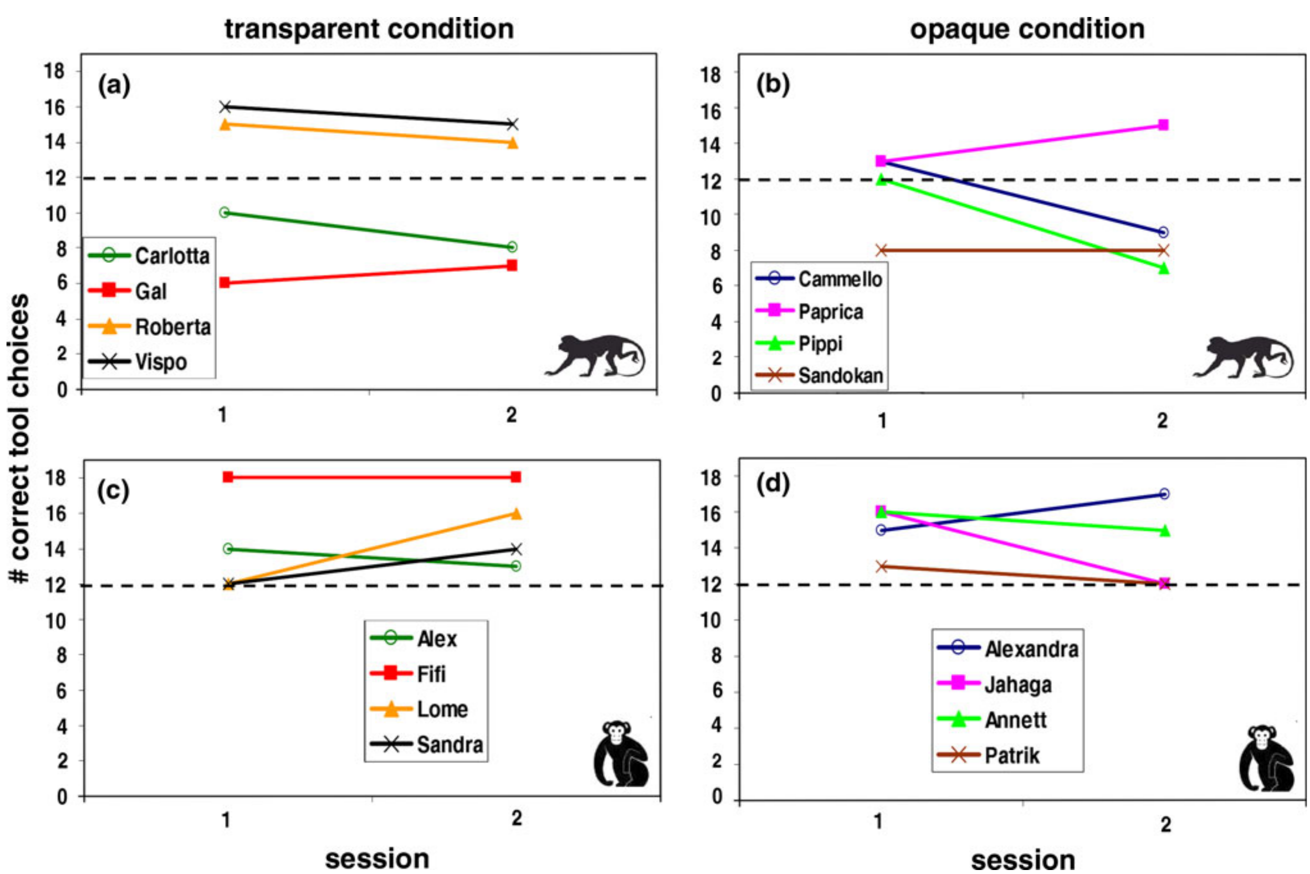

Fig. 7 Number of correct trials across 18-trial sessions in transfer of Phase 2 for capuchins (**a**, **b**) and chimpanzees (**c**, **d**) in transparent and opaque conditions. The *dotted lines* represent significance levels

the second transfer test, suggesting that they used the relational rule of selecting the longest stick, which supports our third prediction. In addition, chimpanzees were faster than capuchins in acquiring this underlying relational rule. Other variables, such as the number of correct choices on the first trials of the transfer tests, did not differ between species. But given our small sample size, caution should be used in asserting that there is no species difference.

A closer look at chimpanzees' and capuchins' differences and similarities is warranted. The appreciation of the functional characteristics of the tools might differ between them because of their different abilities at recognizing, storing, and retrieving relevant information, concerning length, while inhibiting irrelevant information concerning the handle. Selecting the longest stick requires replacing the prepotent response (selecting the handle associated with the reward) with a different strategy (selecting the longest stick among the available ones). This challenge can be conceived as one of inhibiting an action and/or of shifting strategy of selection (Kenemans et al. 2005; Spencer et al. 2001). This is also difficult for young children, who primarily attend to surface or featural similarity when comparing two objects or situations. Only later, as children acquire knowledge, do they shift their attention to the relational similarity (Gentner and Rattermann 1991). Gentner et al. (1995) reported that 6-year-old children, asked to interpret the metaphor "a tape recorder is like a camera", used object-based interpretations (e.g. "both are metal and black"), whereas 9-year-old children noticed the relational structure of the metaphor, namely the ability to record something for later. Moreover, older children are more successful in ignoring an object match in favour of a relational match (Loewenstein and Gentner 2005; Paik and Mix 2006; Richland et al. 2006). In the study on analogical reasoning by Kennedy and Fragaszy (2008), capuchin monkeys were able to ignore a featural match (i.e. a cup of the same absolute size) and preferentially selected a cup of the same relative size. However, to learn to attend to the relative size of cups, capuchins received considerable training and their learning speed was much slower than chimpanzees (Flemming and Kennedy 2011).

Moreover, chimpanzees outperform capuchins in tasks placing high loads on working memory (e.g. Amici et al. 2010), as well as in attention management. Fragaszy et al. (2009) proposed an ecological perspective to explain the latter difference; capuchins, as smaller animals with a higher risk of predation than chimpanzees, are more "vigilant" and interrupt their activity every few seconds to look around themselves. In captivity, where predators are absent, capuchins are still "vigilant" while working on experimental problems and often interrupt their ongoing activity. Chimpanzees seem to do it less frequently. Since our experiment included distracters and the tool was selected at some distance from where it was used, focused attention certainly played a role. Vigilance decreases focused attention, which may have weakened capuchins' ability to monitor and learn from the outcome of their actions in our study.

In previous studies (Cummins-Sebree and Fragaszy 2005; Fujita et al. 2003), capuchins selected tools on the basis of functional characteristic (e.g. affordances and/or spatial arrangement of tool and food), disregarding non-functional features (e.g. colour, shape, size, or texture of the sticks). After intensive and varied training, capuchins also learned to solve 3-term problems involving food, tool, and type of hindrance (Fujita et al. 2011). These results seem to contradict ours in which capuchins were not quickly successful in tool selection. However, it should be noted that the complexity of our task exceeds that of the those described since (1) the subject has to produce and keep track of the spatial relations between the elements of the task (stick, tube, and reward) instead of exploiting the one prearranged by the experimenter and (2) the non-functional feature (handle) is very salient, providing both tactile and visual information, and shape and colour cues may be easier to detect than length. Overall, the handle was more salient and confusing for capuchins than for chimpanzees possibly because of perceptual and/or attentive factors. Studies on the perception of hierarchical visual stimuli (i.e. stimuli consisting of a large global shape formed by the spatial arrangement of small local shapes) have demonstrated that monkeys faced with hierarchical patterns discriminate the local components of the stimuli more proficiently than their global structure (e.g. capuchins: Spinozzi et al. 2003; baboons: Fagot and Deruelle 1997). In contrast, chimpanzees do not always process the local features of the hierarchical stimuli faster than their global shape (Hopkins and Washburn 2002; Fagot and Tomonaga 1999). Therefore, capuchins' locally oriented perception of visual stimuli could have biased them to learn about local and salient perceptual features, such as the shapes/colours of the handles. Moreover, chimpanzees could have outperformed capuchins because of their ability (1) to process the problem as a whole and to take into account multiple features and/or (2) to take into account functional and non-functional characteristics of the three tools concurrently. Also, since the tools were longer in relation to body size for capuchins than for chimpanzees, future studies should elucidate whether chimpanzees would outperform capuchins when tool length is scaled according to body size.

Another important finding of our study concerns the effectiveness of experience with varied stimuli. Most capuchin monkeys and one chimpanzee learned to take into account the tool's functional feature when exposed to sticks of different lengths that could each be matched with each handle, while they did not when exposed to tools having a stable length–handle association. With the latter procedure (used in Phase 1), these subjects learned associations (e.g. choose the white handle and be rewarded) that may turn out to be wrong in the transfer test. In contrast, the varied-association procedure (used in Phase 2) promotes the acquisition of a relational rule based on the functional feature and prevents the acquisition of rules based on non-functional ones. Thus, our results support the idea that varied experience is fundamental to constructing flexible knowledge, as has also been demonstrated in the visual cognition of captive non-human primates and pigeons, for which training with a large and varied set of stimuli allows better acquisition of abstract concepts (Katz et al. 2007; Truppa et al. 2010, 2011; Wasserman and Bhatt 1992).

In contrast with our second prediction, neither capuchins nor chimpanzees performed better when they could observe the functioning of the tool (and consequently the role played by length to reach and displace the reward) than when they did not. This indicates that visual access to the inner mechanism of the apparatus was not necessary for the solution and that using the relational rule of "always select the longest stick" was sufficient to be successful. In this respect, chimpanzees were quicker than capuchins in reaching the learning criterion and were already successful in Transfer 1. It is likely that chimpanzees were better able than capuchins to encode the length rule and its outcome in terms of reward even in the absence of visual feedbacks. Interestingly, 2-year-old children, tested in a task similar to ours, chose the correct stick more often in the transparent than in the opaque condition in the transfer of Phase 1 (Bechtel 2011). However, in both conditions, preference for the longest (correct) tool did not occur in trial 1. In particular, both tools were chosen equally in the transparent condition, whereas the short tool was preferred to the longest one in the opaque condition. Hence, children who received visual feedback from the behaviour of the tool in relation to the reward were better able to solve the problem than children who did not.

Our study highlights how capuchins and chimpanzees differ in their ability to discern functional and non-functional characteristics of tools and the importance of encountering varied experience for the formation of relational strategies. Future research should compare the performance of capuchins and chimpanzees (and other species) on problems designed to further distinguish among the possible factors leading to differences in tool features processing, for example inhibitory control, attention shifting, working memory capacities, encoding strategies.

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