




1 **Great apes (*Pan troglodytes*, *Pan paniscus*, *Pongo abelii*) exploit better the information**
2 **of failure than capuchin monkeys (*Sapajus* spp.) when selecting tools to solve the same**
3 **foraging problem**

4

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16 We thank the Fondazione Bioparco and Leipzig Zoo for hosting the Primate Centres
17 where the experiments were carried out, and the reviewers and the editor for the useful
18 comments. We declare no competing interests. We declare that the experiments performed in
19 our study complied with Italian and German laws regulating animal care and use. Data and
20 materials will be available upon request.

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25

Abstract

26 In a previous study chimpanzees, bonobos, orangutans, and capuchin monkeys faced a task
27 that required the use of a rigid stick-like tool to displace an out-of-reach food reward, which
28 was located outside the cage either hanging on a string (e.g. apes) or on a table (e.g.
29 capuchins). Three unfamiliar stick-like tools were placed on a wooden platform for the
30 subjects to choose. Testing consisted of two consecutive trials, each with the same set of
31 tools. Before selection subjects learned about the rigidity of the tool either by handling the
32 tools (manipulation), or by observing an experimenter bending and unbending them in
33 sequence (observation); or did not receive any information since the three tools were
34 presented lying on the platform (visual static). In the current study, we investigated whether
35 failing to select the right type of tool in the first trial affected subjects' choices in the second
36 trial. Results showed that when information about the tool rigidity was obtained before
37 selection, great apes and capuchin monkeys changed options in their second choices.
38 However, in the visual static condition, where no information about the rigidity of the tools
39 had been provided before their selection, only great apes discarded wrong tool exemplars in
40 their second trials benefitting from their own mistakes. In contrast, capuchin monkeys did
41 not. We argue that lower attentional focus and lack of stimuli distinctiveness might account
42 for capuchins monkeys' failure to benefit from their own experience.

43

44 Keywords: attention, tool choice, tool use, perseveration, primates

45 Tool use requires the user to encode the properties of objects in relation to other
46 objects (Call, 2000). The actor establishes a relationship between an object (the tool) and
47 other object(s) and/or surface(s) by producing specific actions in order to achieve a goal
48 (Visalberghi & Fragaszy, 2012). Great apes, particularly chimpanzees and orangutans, and
49 capuchins are proficient tool users (Sanz, Call & Boesch, 2013; Visalberghi, Sabbatini,
50 Taylor & Hunt, 2017). Like chimpanzees, capuchin monkeys use stones as a hammer to crack
51 nuts, which they position on hard surfaces (“anvils”) and quickly learn in nut-cracking tasks
52 to attend to the mass of tools and to select heavier stones as hammers (Schrauf, Call, Fuwa &
53 Hirata, 2012; Schrauf, Huber & Visalberghi, 2008). Visalberghi, Fragaszy, and colleagues
54 demonstrated that capuchins also considered several causally relevant features when selecting
55 tools (i.e., mass of the stone, friability, distance to transport, features of the anvils; Fragaszy,
56 Greenberg, Visalberghi, Ottoni, Izar & Liu, 2010; Fragaszy, Pickering, Liu, Izar, Ottoni &
57 Visalberghi, 2010; Liu, Fragaszy, Wright, Izar & Visalberghi, 2011; Massaro, Liu,
58 Visalberghi & Fragaszy, 2012; Visalberghi, Addessi, Truppa, Spagnoletti, Ottoni, et al.,
59 2009). However, there are also notable species differences. For example, in a task to assess if
60 capuchin monkeys and chimpanzees are attentive to the functional, causally relevant features
61 of tools, they were trained to insert a stick into a tube to obtain a reward hidden inside the
62 tube (Sabbatini, Truppa, Hribar, Gambetta, Call & Visalberghi, 2012). The animals could
63 choose between sticks of different lengths (with only the longest stick long enough to reach
64 the reward) and different handles. During a transfer phase, the handles were switched
65 between the tools. Only the chimpanzees attended to the functional features and continued to
66 use the tool with the appropriate length, whereas the capuchin monkeys needed considerably
67 more training to do so. These limitations are in contrast to the monkeys’ performances in the
68 nut-cracking tasks mimicking a natural foraging situation. New solutions to physical
69 problems involve not only background knowledge about object properties, but also an ability

70 to use that information to predict what they can accomplish with an object if they use it as a
71 tool.

72 In a previous series of experiments, chimpanzees, bonobos, orangutans, and capuchin
73 monkeys faced an apparatus problem (see Manrique, Gross & Call, 2010; Manrique,
74 Sabbatini, Call & Visalberghi, 2011) that required the use of a rigid stick-like tool to displace
75 an out-of-reach food reward. Three unfamiliar stick-like tools were placed on a wooden
76 platform for the subjects to choose. Testing consisted of two consecutive trials, each with the
77 same set of tools. Before selection subjects could learn about the tool rigidity properties
78 either by handling the tools themselves (manipulation), or by observing an experimenter
79 bending and unbending them in sequence (observation); or did not receive any information
80 since the three tools were presented lying static on the platform before selection (visual
81 static). All species tested were highly accurate in selecting the appropriate tool (rigid) that
82 met the task requirements in the manipulation and observation conditions. In contrast, all
83 species failed to select appropriate tool exemplars in the visual static condition, where no
84 direct or indirect information about tools' rigidity could have been gathered. Choice in the
85 first trial was successfully guided by the visuo-tactile exploration of the tool or by the
86 observation of manipulation of the tool by the experimenter and only after selection subjects
87 could evaluate whether the rigidity of each tool matched the task requirements. Absence of
88 visuo-tactile exploration or observation of tool manipulation by the experimenter led to
89 selection at chance level in the first choice. Only after having chosen one of the tools,
90 subjects could determine its suitability.

91 To evaluate the putative differences in the tool using abilities of capuchin monkeys
92 and great apes, it may be useful to investigate how the different species use the information
93 gained during success and failure to inform their next choice. In this study we investigated
94 whether great apes and capuchin monkeys changed their choice on the second trial as a

95 function of whether they had selected a correct or incorrect tool exemplar in the first trial
96 with each tool-set in the manipulation, observation and visual static conditions of Manrique et
97 al.'s 2010 and 2011 experiments.

98 **Methods**

99 *Subjects*

100 Great ape subjects were those who had participated in Experiment 2 of Manrique,
101 Gross and Call (2010): 6 orangutans (*Pongo abelii*), 8 chimpanzees (*Pan troglodytes*), and 4
102 bonobos (*Pan paniscus*) housed at the Wolfgang Köhler Primate Research Center in Leipzig
103 (Germany). In total, there were 6 males and 12 females ranging from 5 to 34 years of age.
104 The capuchin monkeys were those who had taken part in Experiment 1 of Manrique et al.
105 (2011): 8 capuchin monkeys (*Sapajus* spp.) housed at the Primate Centre of the Institute of
106 Cognitive Sciences and Technologies, C.N.R. in Rome (Italy). They were 5 males and 3
107 females ranging in age from 9 to 29 years.

108

109 *Materials*

110 For the current paper, we re-analysed videos which we had recorded for our studies in
111 2010 and 2011 (Manrique et al., 2010, and Manrique et al., 2011). For more details on
112 subjects, apparatuses and procedure used see Manrique et al., 2010 and Manrique et al., 2011.

113

114 *Design and procedure*

115 In the original studies, we had presented great apes and capuchin monkeys with an
116 out-of-reach food reward which they could retrieve using a stick-like tool. The appropriate
117 tool needed to be rigid as the reward consisted of a slice of banana (deposited on a table
118 outside the cage with friction curtailing its movement) or a bunch of grapes (hanging from a
119 string outside subject's cage), and subjects had to transmit force from the tool to the food

120 item in order to bring it into reach. Subjects were faced with a platform containing three
121 stick-like tools, only one of which had the appropriate rigidity to meet the requirements of the
122 relevant task. Subjects were given two consecutive trials with the same tool set, in which they
123 were to select one of the tools from the full set to gain access to the food reward. We
124 presented 9 different three-tool sets, thus minimizing the repetition of trials with each tool set.
125 Two trials per tool-set were administered, 18 trials in total for each subject. Selecting the
126 correct tool at above-chance levels indicated that subjects judged the appropriateness of a tool
127 (e.g. rigidity) to solve the task before using it. Before making their first choice, subjects were
128 given information regarding the rigidity of each tool type by 1) allowing them to handle each
129 of the tools in turn before the apparatus was baited (manipulation condition; 3 tool sets) or 2)
130 demonstrating the properties of each tool by bending them for five seconds in front of the
131 subject (observation condition; 3 tool sets). As a control, there was a third condition (visual
132 static; 3 tool sets) in which no handling or demonstration took place, and the three tools were
133 presented in a static position on the platform before subjects could choose. To avoid
134 involuntarily cuing (e.g. Clever Hans effect) the subjects to the correct tool exemplar in each
135 set, the experimenter always pushed the platform containing the three tools while keeping
136 his/her eyes shut until the platform collided with the cage mesh and subjects could point to
137 the desired tool in the set. We ensured that the tools in each set were all perceptually different
138 and that the specific features (e.g. color, texture, diameter, etc.) of the successful tool also
139 varied from one tool set to the next, to avoid the possibility that subjects selected tools based
140 on their surface features rather than their rigidity. The time between gathering information
141 about the tools and using them as well as the inter-trial interval, which lasted approximately
142 3-5 minutes, was comparable between great apes and capuchins.

143 In the original 2010 and 2011 studies we were mainly interested in subjects' ability to
144 choose the correct tool, so we had focused on successful trials only. In order to investigate the

145 cognitive strategies that subjects used to solve the problem, we now scored first-trial
146 successes and errors and coded whether subjects would select a different tool or continue
147 choosing the same one in the second trial as a result of the outcome of the previous trial. In
148 the original studies, we always conducted two consecutive trials with each tool set - a feature
149 that allowed us to investigate whether subjects changed their tool choices in the second trial
150 after having selected the wrong tool in the first trial. Changing tools in the second trial after
151 an initial wrong choice would be indicative of a two-step gathering of information (1st step:
152 their own haptic inspection of each tool or observation of the handling by the experimenter –
153 and 2nd step when actually using the chosen tool in relation to the food). It is conceivable that
154 memory demands could influence the accuracy of the choices because subjects had to
155 remember the properties of each tool prior to their choice and perhaps more importantly,
156 which tool they had selected in their first trial.

157 Since Manrique et al. (2010) found no differences between chimpanzees, bonobos and
158 orangutans in their ability to choose appropriate tools as a function of their rigidity, we
159 pooled the data of the three ape species for our current analysis. We separated trials in which
160 subjects collected information about the rigidity of the tools before selecting one
161 (manipulation + observation condition trials) from those in which they had remained ignorant
162 (visual static condition). This distinction was made because in the previous 2011 study,
163 capuchin monkeys were especially perseverative in the visual static condition, where no
164 information of the tools' rigidity was provided before selection, which points to lack of
165 information as the possible cause for perseveration. The visual static condition offered
166 information about the tools' appropriateness only after one tool had been selected and tried in
167 the apparatus, while the other two conditions offered information about the tools'
168 appropriateness before and after one tool had been selected and tried in the apparatus. The
169 comparison between the visual static condition and the manipulation + observation conditions

170 allowed us to assess how the apes and capuchins made use of the information available in two
171 stages (previous to-and-after selection). The main independent factors investigated were the
172 taxa (great apes and capuchin monkeys) and the information provided before selection
173 (manipulation + observation – hereafter, information - vs visual static). The main dependent
174 variable investigated is number of changes in the tool selected in the second trials after
175 correct and incorrect choices. In other words, we wanted to assess whether having failed in
176 the selection of the appropriate tool in the first trial would prompt subjects to disregard that
177 tool and try a different one in the subsequent trial, and whether their choice of tools in the
178 second trial would be influenced by the knowledge of the tool properties that subjects
179 possessed before. The percentages of choices after correct and incorrect choices in the
180 information and no information conditions were not normally distributed (K-S test, all $ps <$
181 0.05). Therefore, we used non parametric statistics to analyze the data. We used the Mann-
182 Whitney test to assess whether apes and capuchins differ in their choice after correct and
183 incorrect responses in both the information and the no information conditions. We used the
184 Wilcoxon signed-rank test to compare switches after correct and incorrect responses within
185 taxa for apes and capuchins in both the information and the no information conditions. After
186 running these initial analyses, we discovered that capuchins, but not apes, were more
187 perseverative (less prone to discarding incorrect tools) in the no information condition.
188 Therefore, we coded the side of the platform selected by capuchins (left, center, right) in the
189 information and no information conditions to detect potential side biases. We also scored the
190 time in seconds that it took them to point to a specific tool in the information and no
191 information conditions to check whether impulsivity played a causal role in capuchins’
192 perseverative responding. We used Wilcoxon exact tests to analyze these additional data.

193

Results

194 Great apes made 53 initial incorrect choices (26 in the information and 27 in the no
195 information conditions) and 85 initial correct choices (75 in the information and 10 in the no
196 information conditions). Capuchins made 32 initial incorrect choices (15 in the information
197 and 17 in the no information conditions) and 40 initial correct choices (33 in the information
198 and 7 in the no information conditions). Figure 1 presents the percent of trials in which
199 subjects changed their tool choice in trial 2 as a function of the outcome of trial 1 (success or
200 failure) in the information and no information conditions for each taxa. Table 1 shows mean
201 percentage of individual switches after correct and incorrect choices in observation,
202 manipulation and visual static conditions. In general, apes switched tools after mistakes and
203 repeated the same choice after successes. Capuchins displayed the same pattern as apes in the
204 information condition, but not in the no information condition. A direct comparison between
205 taxa in the no information condition revealed that apes were more likely than capuchins to
206 switch after a mistake (Mann-Whitney test: $U = 24$, $N_{\text{cap}} = 8$, $N_{\text{apes}} = 15$, $p = 0.013$, see Figure
207 1). Although numerically, capuchins were more likely to switch than apes after a correct
208 choice, this difference was not significant (Mann-Whitney test: $U = 10.5$, $N_{\text{cap}} = 5$, $N_{\text{apes}} = 8$,
209 $p = 0.083$, see Figure 1). In the information condition, apes and capuchins did not differ in
210 percentages of switches after a correct (Mann-Whitney test: $U = 48.5$, $N_{\text{cap}} = 8$, $N_{\text{apes}} = 17$, p
211 $= 0.104$) or an incorrect choice (Mann-Whitney test: $U=29$, $N_{\text{cap}} = 6$, $N_{\text{apes}} = 12$, $p = 0.470$,
212 see Figure 1).

213 Apes switched significantly more often after initial incorrect choices than after initial
214 correct choices both in the information (Wilcoxon signed-rank test: $T = 0$, $N = 12$, $p = 0.005$)
215 and in the no information conditions (Wilcoxon signed-rank test: $T = 0$, $N = 8$, $p = 0.028$).
216 Capuchins also switched more often after initial incorrect choices than after correct choices in
217 the information condition (Wilcoxon signed-rank test: $T = 0$, $N = 6$, $p = 0.043$) but, unlike

218 apes, they did not switch in the no information condition (Wilcoxon signed-rank test: $T = 1.5$,
219 $N = 5, p = 0.414$).

220 -----

221 Figure 1

222 Table 1 around here

223 -----

224 We found no significant differences in the tool position preferred by capuchins as a
225 function of condition (Wilcoxon tests: Left: $U = 15, N = 5, p = 0.063$; Center: $U = 19, N = 6$,
226 $p = 0.125$; Right: $U = 21, N = 7, p = 0.328$). Additionally, we found no significant difference
227 between conditions on the average time that capuchins took to select one tool on the platform
228 (Wilcoxon test: $U = 5, N = 7, p = 0.156$).

229

230 Discussion

231 Great apes followed a win-stay, lose-shift strategy with regard to tool selection,
232 switching tools after failures and selecting the same tool after successes. They did so both in
233 the information and in the no information condition, i.e., regardless of the amount of
234 information about the tool properties that they gathered prior to their first tool choice.
235 Capuchin monkeys also followed a win-stay, lose-shift strategy when they gathered tool
236 property information prior to their first choice in the information conditions (i.e., in the
237 observation-manipulation condition), but not when they gathered no information (i.e., in the
238 visual-static condition). Unlike apes, capuchin monkeys did not learn from their own tool
239 selection mistakes (in trial 1) unless they already possessed previous information about the
240 tools' properties. The behavior of capuchin monkeys in the no information condition where
241 they do not behave differently when correct than when wrong in first trial (see Figure 1) is

242 almost a mirror image of what we see in great apes (see Figure 1). Next, we discuss these
243 findings and their implications.

244 A careful inspection of the videos revealed no specific superficial tool features (e.g.
245 color) that could account for the capuchins' choices, suggesting that their perseverative
246 responding was not caused by poor perceptual discrimination. The tools in each set were
247 different from each other and we observed no systematic preferences for a particular color,
248 texture or shape that would indicate a specific preference for a superficial tool feature
249 (besides rigidity). Side biases in the absence of relevant tool rigidity information also did not
250 seem to explain the perseverative responding of capuchins because we observed no
251 significant side preferences. Lastly, we found no significant difference in the time it took
252 capuchins to select a tool between conditions, suggesting that impulsivity (in the absence of
253 relevant information about tool rigidity) did not seem to explain the behavior of capuchins
254 either.

255 De Lillo and Visalberghi (1994) investigated capuchins' learning strategies using the
256 transfer index (TI) and mediational learning (ML) paradigms. The TI is a discrimination
257 reversal task in which there are two stimuli A and B. Initially A is rewarded and B is not
258 (A+B-) until the subject reaches a given success criterion; then the reward contingencies are
259 reversed (A-B+). Success in the TI can be achieved by stimulus-response associative
260 learning, or by the feedback information given by the rewarded/unrewarded choices, where
261 learning can be mediated by the formation of a rule that suits the specific requirements of the
262 task, i.e., win-stay (choose again the same objects) vs lose-shift (choose the other object). The
263 ML paradigm allows to clarify the process underlying success in the TI. De Lillo and
264 Visalberghi (1994) demonstrated that capuchins perform well in the TI task and that their
265 performance is not based on mediational learning, as it is the case for chimpanzees
266 (Rumbaugh & Pate, 1984). Thus, one explanation for the difference between capuchin

267 monkeys and apes in our tool-using study is that the former may not be able to quickly
268 benefit from their own mistakes. However, there are reasons for rejecting this explanation.
269 Capuchin monkeys can learn to select appropriate tools and how to use them after a trial and
270 error process with the speed of learning depending on how many features of the elements of
271 the task and spatial relations among these elements they have to take into account
272 (Visalberghi & Fragaszy, 2012). In our study, capuchins consistently selected a new tool
273 when their first choice was wrong only if they had gathered information about tool properties
274 prior to tool selection. Moreover, capuchin monkeys that had selected the correct tool in trial
275 1 (thus succeeded in obtaining the food reward) did not seem to consistently select it again in
276 trial 2 in the no information condition. Overall, these data suggest that rather than mistakes
277 per se, capuchin monkeys' difficulties may be related to the lack of prior information about
278 tool properties prior to their initial selection of a tool.

279 Our main finding is that capuchins benefited more from receiving prior information
280 about tool properties than information gathered only while using the tool. This is surprising
281 given that learning about tool properties in the same context where such information must be
282 used, would seem to be more relevant than obtaining that same information in a different
283 context. Given the importance of executive function for tool-use, we next turn our attention
284 to various aspects of executive function in an attempt to explain this finding.

285 First, there is the issue of attentional focus and especially the potential distracting
286 effect of food presence. During the prior information conditions, subjects manipulated or
287 witnessed the manipulation of the tool, thus they acquired some information about tool's
288 properties including rigidity. Crucially, in the prior information phase the tool was never put
289 in relation to the task or displayed in the presence of food. In contrast, after selecting the tool
290 the subject attempts to extract the food located inside the apparatus with the tool chosen. One
291 could argue that the absence of the food or the task allowed subjects to exclusively focus their

292 attention on the tool's properties whereas in the first trial in which they use the tool, subjects
293 may have divided their attention between the food, the apparatus and the tool, and the
294 relations among them. Indeed, multiple loci of attention may have prevented capuchin
295 monkeys from focusing on the tool properties coming from the manipulation, thus
296 compromising their ability to correct their tool selection mistakes in the following trial.
297 Capuchins have already shown poorer abilities than chimpanzees in encoding the properties
298 of objects in relation to other objects and have required more varied and contrasting
299 experience to attend to the functional feature of the tool when selecting among three tools in
300 order to extract food from a tube (Sabbatini et al., 2012). Birch (1945) used an analogous
301 argument to explain why a group of chimpanzees that experienced free play with objects
302 performed better at a subsequent tool-use task compared to a group that did not experience
303 such exploratory period. Our prior information conditions may have provided relevant
304 information as the exploratory period in that other study.

305 Second, there is the issue of working memory and tool distinctiveness. Without the
306 benefit of functional information about the tools, the only information available is their
307 physical appearance. It is known that successful visual discrimination requires either
308 multiple trials with a single stimuli set or repeated presentations of multiple stimuli sets to
309 obtain an optimal (trial 1) performance (e.g. Harlow, 1949). Moreover, tactile information
310 increase capuchins' learning speed for visual discrimination of object features and the
311 acquisition of tactile information about object features is advantageous allowing capuchins to
312 achieve faster high levels of visual accuracy (Carducci, Squillace, Manzi & Truppa, 2020);
313 this indicates that information from touch enhances object recognition in the visual modality.
314 Although discriminability is aided by the number of distinct dimensions along which stimuli
315 differ, in our experimental procedure some of these dimensions (e.g., length) were
316 purposefully equated. Nevertheless, in the information condition these tool features became

317 more distinctive when the subjects or the experimenter manipulated the tools. Without prior
318 information, remembering the tool that has been selected in the preceding trial might be
319 difficult. Both for correct and incorrect first choices; this is precisely what our results
320 indicated. In turn, without the benefit of prior information, subjects did not consistently
321 avoid the incorrect tool or selected the correct tool in trial 2. Memory limitations per se do
322 not seem to satisfactorily explain the behaviour of capuchins in the current study because in
323 previous studies capuchin monkeys selected and transported appropriate tools to an apparatus
324 located outside the context of tool gathering, and hence retained simultaneously the
325 information of task requirements and tool affordances in memory until they completed the
326 task (Judge & Bruno, 2012).

327 Third, there is the issue of inhibitory control and pre-existing biases that might have
328 been difficult to overcome in the absence of competing evidence. Once capuchins selected a
329 tool in trial 1 of the no information condition, they may have continued to select it even if it
330 proved ineffective because they had no way of assessing whether other tools might work
331 better than the chosen one. According to this explanation, tool manipulation (or vicarious tool
332 manipulation) prior to tool selection may have offered the information required to abandon
333 the ineffective tools. This “excessive rationality” may be further strengthened if capuchins’
334 choices were not random, but denoted a pre-existing preference for one of the tools, or having
335 selected a given tool would have induced a cognitive bias, such as the endowment effect (i.e.,
336 individuals value what they currently possess more than an identical alternate option;
337 Kahneman, Knetsch & Thaler, 1990), or loss aversion (i.e., individuals are more averse to
338 losses than to similarly sized gains; Kahneman, Knetsch & Thaler, 1991). Capuchins have
339 these biases towards food items (e.g. Brosnan, Jones, Lambeth, Mareno, Richardson &
340 Schapiro, 2007; Chen, Lakshminarayanan, & Santos, 2006; Lakshminarayanan, Chen, &
341 Santos, 2008) but data in contexts other than food are lacking so far. We can rule out that

342 capuchins had a side bias, as we failed to find any significant side preferences in the
343 information and/or the no information conditions.

344 Persistent and varied manipulation of objects is a typical characteristic of capuchin
345 monkeys (Truppa, Carducci & Sabbatini, 2019). But persistence, continuing to try to reach a
346 goal even when doing so becomes difficult and drawn out, is considered different from
347 perseveration, continuing a behavior when it ceases to be effective or rewarding, as
348 perseveration apparently serves no adaptive purpose (Cepeda & Munakata, 2007; Serpell,
349 Waller, Fearon, & Meyer, 2009). It has been suggested that the inability to inhibit responses
350 may manifest itself in repetitious behavior and an inability to extinguish a learned behavior in
351 favor of a novel response (Judge, Evans, Schroepfer, & Gross, 2011). Thus, one can also
352 hypothesize that incomplete information and the inability to encode relevant features when
353 there are multiple loci of attention may favor perseverative behavior instead of persistent
354 ones in capuchin monkeys.

355 Taken together, we favor attentional focus and lack of stimuli distinctiveness as
356 complementary explanations for capuchins monkeys' failure to quickly benefit from the
357 feedback gained in first trials to perform a better choice in the second trial. We see at least
358 two possibilities for explaining apes' superior performance compared to capuchins. One
359 possibility is that they were better than capuchins at visual discrimination regardless of tool
360 functional properties. They selected a tool by its appearance and if it worked they re-picked
361 it in the next trial but if it did not work, they changed their choice. We think that this is
362 unlikely given that apes often ignore superficial features but not functional ones (Hanus &
363 Call, 2008; Manrique et al., 2010). Another possibility is that apes possess enhanced
364 executive functions compared to capuchins that made them less vulnerable to a lack of
365 information about tool properties prior to selecting and using tools. In this particular task,
366 apes may have been able to extract and retain information about functional features while

367 using the tools due to their greater ability to focus on multiple loci and their relations.
368 However, it is important to highlight that their proficiency is not unlimited; in fact, when they
369 had to plan multiple steps to solve a new problem and use a tool simultaneously they also
370 struggled (Voelter & Call, 2014).

371 In conclusion, our previous studies showed that either manipulating tools or observing
372 a human manipulate tools helped apes and capuchin monkeys to select the most suitable tool
373 in a subsequent tool-using task even though tools had not been previously associated with the
374 task or the food reward. Our current analysis complements those findings by showing that
375 capuchin monkeys' selection of a suitable tool in the second trial benefited more from tool
376 exploration and vicarious exploration (i.e., observation) than from the actual feedback of
377 using the chosen tool in trial one. Our findings further highlight that capuchin monkeys,
378 unlike apes, seemed unable to immediately benefit of their own mistakes to be able to select a
379 better tool in trial 2 when they lacked prior information about tool properties. In contrast,
380 apes used the outcome of their first trial to either switch (failure) or maintain (success) the
381 same tool choice in the next trial. Apes' greater flexibility and versatility in the use of the
382 feedback obtained in trial 1 (success or failure) compared to capuchin monkeys promises to
383 be a fruitful avenue of research.

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485 **Figure caption**

486 **Figure 1.** Median percentage (+ IQR) of switching to a different tool in the second trial as a
487 function of the outcome in the first trial for capuchins and apes in the information and no
488 information conditions. Median percentages of switches after success in the first trial are
489 depicted in dark blue and median percentages of switches after failure in the first trial are
490 depicted in orange. P values of statistical comparisons of percentage of switching between
491 capuchins and apes after success and failure in the information and no information conditions
492 are reported.

493

494 **Table 1**

495 Mean percentage of individual switches after correct and incorrect choices in observation,
 496 manipulation and visual static conditions. Median and IQR for each species for separate, as
 497 well as together for apes, are reported.

	Species	Observation condition		Manipulation condition		Visual static condition	
		Mean % switches after correct choice	Mean % switches after incorrect choice	Mean % switches after correct choice	Mean % switches after incorrect choice	Mean % switches after correct choice	Mean % switches after incorrect choice
	Fraukje chimpanzee	0		0	50		67
	Frodo chimpanzee	0		0		0	100
	Jahaga chimpanzee	0		0	0	0	100
	Patrick chimpanzee	0	100	0	100		100
	Tai chimpanzee	0	100	0			
	Trudi chimpanzee	0	0	0			100
	Ulla chimpanzee			0	50		0
	Median chimpanzee	0	67	0	50	0	100
	IQR chimpanzee	0	75	0	25	0	25
	Bimbo orangutan	50	100	0			
	Dokana orangutan	0		0		0	0
	Dunja orangutan	33		50	100		67
	Kila orangutan	0	50	0	0	100	100
	Padana orangutan	0	100	0	100	0	100
	Pini orangutan	0		0		0	100
	Median orangutan	0	100	0	100	0	100
	IQR orangutan	25	25	0	50	25	33

Joey	bonobo	0	100	0			100
Kuno	bonobo	0		0		0	100
Limbuko	bonobo	0	100	0	0	0	100
Yasa	bonobo	0		0			
Median	bonobo	0	100	0	0	0	100
IQR	bonobo	0	0	0	0	0	0
Median	Apes	0	100	0	50	0	100
IQR	Apes	0	50	0	100	0	25
Carlotta	capuchin	100	100	0	100		67
Gal	capuchin	0		0	100	0	50
Pedro	capuchin	67		67			0
Pepe	capuchin	0		0			33
Pippi	capuchin	0	100	100	100	100	100
Roberta	capuchin	0	100		67	100	0
Robin Hood	capuchin	0	0	0		0	0
Vispo	capuchin	0	100	0	100	100	50
Median	capuchin	0	100	0	100	100	42
IQR	capuchin	8	0	33	0	100	54