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## 2 **Younger apes and human children plan their moves in a maze task**

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## Abstract

Planning defined as the predetermination of a sequence of actions towards some goal is crucial for complex problem solving. To shed light on the evolution of executive functions, we investigated the ontogenetic and phylogenetic origins of planning. Therefore, we presented all four great apes species (N=12) as well as 4- and 5-year-old human preschoolers (N=24) with a vertical maze task. To gain a reward placed on the uppermost level of the maze, subjects had to move the reward to the bottom through open gaps situated at each level of the maze. In total, there were ten gaps located over three of the maze's levels, and free passage through these gaps could be flexibly blocked using multiple traps. Due to the decision tree design of the maze, the subjects had to plan their actions depending on the trap configuration up to two steps ahead to successfully retrieve the reward. We found that (1) our measure of planning was negatively correlated with age in nonhuman apes, (2) younger apes as well as 5-year-old children planned their moves up to two steps ahead whereas 4-year-olds were limited to plan one step ahead, and (3) similar performance but different underlying limitations between apes and children. Namely, while all species of nonhuman apes were limited by a lack of motor control, human children exhibited a shortage in shifting their attention across a sequence of subgoals.

Keywords:

Primates, Planning, Problem solving, Executive functions, Aging, Inhibitory control

## 40 Introduction

41 While thinking about the next move, a good chess player not only needs to envision the  
42 potential outcomes of the current move but also to conceive of the sequences of multiple  
43 upcoming moves to determine what to do next (e.g. Charness, 1981). Even more mundane  
44 activities such as getting dressed or cooking a meal entail the planning of a number of actions  
45 before the execution of the first action. Accordingly, planning has been defined as the  
46 “predetermination of a course of action aimed at achieving some goal” (Hayes-Roth & Hayes-  
47 Roth, 1979).

48 Such strategic planning is essential for complex problem solving. In the problem-solving  
49 literature, an important distinction has been made between forward search on the one hand and  
50 problem-reduction or “subgoaling” on the other hand (Willatts, 1989). In forward search, a  
51 sequence of actions or choices is tried out step by step, a strategy that has also been termed  
52 “generate and test” (Klahr, 1994). If an error occurs, an alternative sequence of actions or  
53 choices is tried out until eventually the goal is achieved. Remembering which sequence of  
54 actions has already been tested to avoid the previously made error can impose significant loads  
55 on memory. Willatts (1989) subdivides forward search into random and heuristic search. In  
56 random search each single decisions is made on a trial-and-error basis. In heuristic search (also  
57 termed "sighting", see Wellman, Fabricius, & Sophian, 1985), the efficiency of search is  
58 increased by the usage of fixed rules (i.e. heuristics like a proximity bias) that guide each single  
59 decision in a sequence.

60 In contrast to forward search, subgoaling involves a means-ends analysis, that includes the  
61 identification of the discrepancy between the current state and the target state and the  
62 consideration of means to reduce this discrepancy (Willatts, 1989). In the simplest version, this  
63 has been called “hill climbing” (Klahr, 1994) in which the next move (but nothing beyond the

64 next move) is evaluated based on a goodness of fit approximation between the current state  
65 and the target state. Subgoaling goes beyond that: if the discrepancy between current state and  
66 goal state cannot be resolved immediately a sequence of subgoals is formulated. Achieving  
67 each of these subgoals in sequence will lead to the overarching goal. The key difference to  
68 forward search is that in subgoaling the sequence of subgoals is predetermined before the first  
69 step is made. Thus, subgoaling includes planning defined as the predetermination of a  
70 sequence of actions whereas forward search has been described as “planful” (Wellman et al.,  
71 1985), meaning that only the current move is taken into account.

72 These strategies are not mutually exclusive and might be both at work in different situations  
73 (Willatts, 1989). Indeed, in some situations forward search might be more efficient than  
74 subgoaling (no or little information on task-specific means-end relations, limited number of  
75 alternatives), whereas in other settings subgoaling might be better suited for solving the problem  
76 (information on causal structure of the task available, large number of possible alternatives).

77 Experimental studies on planning in children have mostly concentrated on navigation tasks  
78 (including maze and route planning tasks) and subgoaling tasks (like the Tower of Hanoi task).  
79 With regard to navigation tasks, a two-dimensional maze paradigm revealed that 4½- to 7-year-  
80 olds were able to plan the complete path through the maze before the first move (Gardner &  
81 Rogoff, 1990). Interestingly, younger children took longer pauses for planning than older ones, a  
82 finding that suggests that planning is more effortful for younger children. In route planning,  
83 children typically need to collect some items distributed in space. To find the shortest route and  
84 to avoid backtracking to locations that were previously visited the children needed to plan ahead  
85 before the first choice was made. Wellman et al. (1984) reported that 4- and 5-year-olds but not  
86 3-year-old children planned one step ahead. The search strategy of the 3-year-olds was best  
87 explained by a heuristic forward search strategy based on perceptual features of the search  
88 array (“sighting”). Additional experiments by Wellman and colleagues (summarized in Wellman

89 et al., 1985) revealed that the search behavior of preschoolers was best explained by a “mixture  
90 of sighting and planning, with planning growing in dominance over the preschool years”  
91 (Wellman et al., 1984). At the age of 5.5 years children’s search behavior could be solely  
92 ascribed to planning and not sighting. Similarly, Fabricius (1988) found that 5-year-olds were  
93 considering alternative routes before the first move and were spontaneously self-correcting  
94 errors. In contrast, 4-year-olds’ performance was best explained by a mixture of sighting (i.e. a  
95 proximity bias) and planning.

96 With regard to subgoalting tasks, Klahr and Robinson (1981, see also Klahr 1994) showed that a  
97 majority of the 4-year-olds confronted with the Tower of Hanoi task reliably planned one step  
98 ahead (beyond the current move). Around one third of the 4-year-olds, however, did not plan  
99 ahead at all (i.e. they considered nothing beyond the current step). In contrast, all 5- and 6-year-  
100 olds planned at least one step, most of them even more steps ahead (between two and four  
101 steps).

102 Non-human primates face various situations in their natural habitat in which this type of planning  
103 would also be advantageous. Activities that potentially involve planning are extractive foraging  
104 including (sequential) tool use (Sanz & Morgan, 2007), locomotion (Bard, 1995), hunting  
105 (Stanford, 1996) or nest building (van Casteren et al., 2012). Sanz and Morgan (2007) reported  
106 the usage of up to three tools used in a hierarchical sequence to open a beehive and to extract  
107 honey by wild chimpanzees (*Pan troglodytes*). Planning might be implicated in this example by  
108 predetermining the appropriate sequence of tools used. However, as we do not know the  
109 learning history of these wild chimpanzees, chaining of previously established behaviors  
110 provides an alternative account here (Epstein, Kirshnit, & Lanza, 1984).

111 Therefore, experimental studies are needed to shed light on primates’ planning abilities. Mainly  
112 two types of studies have been used to investigate planning: navigation tasks (including route

113 planning and mazes) and serial ordering tasks. First of all, with regard to navigation tasks,  
114 Menzel (1973) pioneered the investigation of chimpanzees' route planning in three-dimensional  
115 space (also known as the traveling salesman problem) by hiding 18 food items randomly in a  
116 large outdoor enclosure and analyzing their search behavior. Menzel showed that the  
117 chimpanzees remembered the location and type of most of the food rewards, but also that their  
118 routes were close to optimum with regard to the food acquisition rate. However, whether the  
119 apes were planning their route in advance or whether they, alternatively, were relying on a  
120 forward search strategy (cf. sighting, Wellman et al. 1985) cannot be distinguished from these  
121 data alone. In vervet monkeys there is evidence that the monkeys considered two further  
122 destinations beyond the current one when deciding for a route (Cramer, 1995; see also Gallistel  
123 & Cramer, 1996). However, a recent re-analysis of Menzel's and Gallistel and Cramer's data  
124 casts doubt on the planning hypothesis (Janson, 2013). Accordingly, the existing evidence for  
125 optimal spatial foraging in primates would not require multi-step route planning but might be  
126 consistent with a forward search strategy based on a proximity bias (in combination with a risk  
127 avoidance strategy).

128 Considering mazes, Bingham (1929) presented chimpanzees with a three-dimensional maze  
129 apparatus and noted that the chimpanzees' behavior involved "preparation for an effect in a  
130 location remote from that where concerted activities are initiated" (p.44). One of the earliest  
131 studies using two-dimensional mazes with great apes was conducted by Rensch and Döhl  
132 (1968) who presented Julia, a juvenile chimpanzee, with a large battery of mazes of increasing  
133 complexity. By means of a magnet the chimpanzee could move a metal ring (that was  
134 previously associated with a food reward) located underneath a Plexiglas panel through a maze.  
135 In the beginning of each trial, Julia had to decide between two maze arms by moving the metal  
136 ring down from an elevation (the elevation prevented her to correct her response). Julia learnt to  
137 inhibit the first move (up to a delay of 75 seconds) until she had tracked the path to the exit of

138 the maze. After having gained considerable experience (2215 trials), Julia reached a  
139 comparable performance to naïve biology students.

140 More recently, Fragaszy and colleagues (2003; 2009; Pan et al., 2011) tested capuchin  
141 monkeys (*Cebus apella*) and chimpanzees with novel two-dimensional alley mazes presented  
142 on a computer screen. Fragaszy et al. (2003) for the first time systematically manipulated the  
143 maze complexity in terms of number of choice points and the directional properties of choices.  
144 Chimpanzees and capuchin monkeys solved more mazes without error than expected by  
145 chance with chimpanzees generally performing better than capuchin monkeys. Chimpanzees  
146 and capuchin monkeys both corrected errors when they had chosen an incorrect path. The  
147 performance of the chimpanzees, in contrast to the monkeys, was independent of the number of  
148 choice points and directional properties of the maze. Therefore, the search behavior of most  
149 monkeys could be explained by a planful forward search based on the heuristic “direction of the  
150 path in relation to the goal”. In contrast, chimpanzees (and one monkey) seemed to consider  
151 upcoming choices in relation to the goal as indicated by smaller error rates towards the end of  
152 the maze. Fragaszy et al. (2003) concluded that chimpanzees and one monkey were able to  
153 consider one choice at a time “and sometimes more”. In the same vein, Iversen and Matsuzawa  
154 (2001) found that in a fingermaze task after training with mazes of gradually increasing  
155 complexity one chimpanzee could solve new mazes without making corrections in about 91% of  
156 the cases. However, when the two paths leading to the target differed in length the chimpanzee  
157 performance dropped to 53%. Thus, the map-reading ability of the chimpanzee in this task was  
158 limited by a preference for the shortest path. Most of these maze studies either involved  
159 extensive training and/or a shaping procedure that involved a gradual increase in maze  
160 complexity with some notable exceptions (Fragaszy et al., 2009; Pan et al., 2011). Another  
161 common feature of most of these alley maze tasks is that they are presented on a computer  
162 screen. Such computerized tasks provide only visual information to the subjects and prevent the

163 subjects from gathering additional information on the task for example by haptically exploring  
164 the mazes. Therefore, such computerized mazes might be less salient to the subjects which  
165 might, in turn, negatively affect their performance.

166 Secondly, serial ordering tasks (also termed sequential chaining; Terrace, 1984) have been  
167 used to assess planning abilities in nonhuman primates (e.g. Beran, Pate, Washburn, &  
168 Rumbaugh, 2004; Biro & Matsuzawa, 1999; Inoue & Matsuzawa, 2007; Kawai & Matsuzawa,  
169 2000; Scarf & Colombo, 2009). In this task a number of stimuli are shown simultaneously on a  
170 computer screen. Subjects are trained to respond to the stimuli in a fixed order. For instance,  
171 Biro and Matsuzawa (1999) trained the female chimpanzee Ai to order three Arabic numerals  
172 ranging from 0 to 9. After training was completed, they introduced so-called switch trials.  
173 Crucially, in these switch trials the location of the second and third numeral was interchanged  
174 after the response to the first numeral. If the chimpanzee already had planned the response to  
175 the second stimulus before or while making her response to the first stimulus, the performance  
176 should drop in these trials. This is exactly what Biro and Matsuzawa (1999) found. Ai increased  
177 her error rate and response times after the location of the second and third stimulus had  
178 changed. Therefore, Ai seemed to have planned one choice ahead before or while the first  
179 move was executed. Meanwhile these results have been replicated with three additional  
180 chimpanzees (Beran et al., 2004), six rhesus macaques (*Macaca mulatta*; Beran et al., 2004;  
181 Scarf, Danly, Morgan, Colombo, & Terrace, 2011), eight capuchin monkeys (*Cebus apella*;  
182 Beran & Parrish, 2012), and partially also with two pigeons (*Columbia livia*; Scarf & Colombo,  
183 2010). In contrast, when switch trials were introduced later in the sequence (interchanging the  
184 location between the third and fourth stimulus) there was no drop in performance in  
185 chimpanzees (Beran et al., 2004) and in rhesus monkeys there was only a drop in performance  
186 in one of four individuals (Scarf et al., 2011). Thus, the planning abilities of chimpanzees and  
187 rhesus macaques seemed to be largely limited to one step in this paradigm (maybe with the



188 exception of one rhesus monkey who seemed to have planned two steps ahead). However,  
189 recent evidence based on eyetracking with long-tailed macaques (*Macaca fascicularis*) on a  
190 similar serial ordering task cast some doubt on whether monkeys engaged in planning while  
191 solving the task (Scarf & Colombo, 2009). Scarf and Colombo found that the increased latency  
192 to respond to the first item in the sequence was not due to scanning the whole array of items  
193 and predetermining multiple responses before the onset of the first response but rather an  
194 artifact of the serial ordering task.

195 Another variation of the serial ordering task consists of masking the stimuli on the screen after  
196 the selection of the first one. Here, the results from different labs are inconsistent: Matsuzawa  
197 and colleagues (Inoue & Matsuzawa, 2007, 2009; Kawai & Matsuzawa, 2000) showed that five  
198 chimpanzees could correctly remember sequences between four and up to seven items. In  
199 contrast, Beran and colleagues (2004) found that two chimpanzees and two rhesus macaques  
200 presented with mask trials remembered only one item beyond the current one whereas one  
201 additional chimpanzee remembered two items. Note however, that successful subjects in  
202 masking trials do not necessarily plan the entire sequence before their first move but encode  
203 and store the presented stimuli in working memory and then respond to one stimulus after the  
204 other without planning ahead (eidetic strategy).

205 In summary, the evidence from all of these experimental studies suggests that even after  
206 extensive training and shaping procedures the planning abilities of nonhuman primates (i.e. for  
207 great apes the evidence is largely restricted to chimpanzees) is limited to one step. Thus, hill  
208 climbing might explain these findings, i.e. while executing the current decision the next step is  
209 already considered by means of a goodness of fit approximation between the outcome of the  
210 current move and the goal state. There is no evidence of the more demanding subgoaling  
211 strategy based on the *predetermination* of a sequence of subgoals, that is, before the current  
212 decision is made. None of the above reviewed studies has examined whether the apes had

213 considered an upcoming choice *before* the current one was made. Such a subgoaling strategy,  
214 however, appears to be crucial for complex, multi-step activities. Furthermore, it is unclear to  
215 what extent the previously identified planning abilities depend on training.

216 With regard to the cognitive substrate, subgoaling includes the representation, maintenance,  
217 updating and hierarchical organization of multiple goals in working memory towards an  
218 overarching goal and the inhibition of (prepotent) actions before the plan is formulated  
219 (behavioral inhibition). Subgoaling therefore involves what has been considered as the core of  
220 executive functions: working memory, cognitive flexibility, and inhibitory control (e.g. Diamond,  
221 2006; Fuster, 2002; Goldman-Rakic, 1987; Kimberg & Farah, 1993; Miyake et al., 2000;  
222 Norman & Shallice, 1980; Roberts & Pennington, 1996; Shallice, 1982). These executive  
223 functions have commonly been related to the frontal lobe in both, humans and monkeys.  
224 Furthermore, it has been suggested that the enhanced cognitive abilities of humans compared  
225 to other primates are based on functional and structural specializations in the prefrontal cortex  
226 (Fuster, 2002; Roth & Dicke, 2005). Interestingly, humans and great apes, however, share a  
227 particularly large frontal cortex (Semendeferi, Lu, Schenker, & Damásio, 2002). At the  
228 behavioral level little is known about the evolution of these executive functions. In the present  
229 study we therefore seek to investigate the phylogenetic and ontogenetic origin of planning  
230 abilities using a comparative approach including human children and our closest living relatives,  
231 the great apes. In particular, we retrace the evolution of the components of subgoaling by  
232 disentangling great apes' and children's limitations in attentional control (shifting attention  
233 across a sequence of subgoals) and motor control (inhibiting prepotent responses).

234 In order to address these issues, we presented all four species of nonhuman great apes (*Pan*  
235 *paniscus*, *Pan troglodytes*, *Gorilla gorilla*, *Pongo abelii*; see Experiment 1) as well as 4- and 5-  
236 year-old human children (see Experiment 3) with a vertical maze apparatus. The task for the  
237 subjects was to negotiate a reward placed on the uppermost level via open gaps located in each

238 level through the maze to one of two exits. While doing so, the subjects had to avoid traps that  
239 blocked some of the openings. We presented twenty-four trial-unique configurations of these  
240 traps to our subjects. Importantly, the maze was organized as a decision tree. A major  
241 advantage of this design was that it allowed us to assess whether and if so, how many  
242 decisions (0-2) our subjects considered beyond their current decision. In addition, the design  
243 enabled us to assess the degree of motor control that guided their performance. Following  
244 Willatts' (1989) definitions described above, we interpreted the predetermination of sequences  
245 of actions as evidence for the usage of a subgoaling strategy. If we could ascribe subjects'  
246 performance solely to a trial-to-trial post-error adjustment (possibly involving the usage of a  
247 fixed heuristic that guides each single decision) this would suggest the usage of a (planful)  
248 forward search strategy.

249 Contrary to most other published studies on planning in nonhuman primates, this paradigm did  
250 not involve prior training or any shaping procedures. Consequently, the current experimental  
251 design allowed us to assess great apes' and children's planning abilities in a more spontaneous  
252 manner. Based on previous research reviewed above, we hypothesized that great apes and 4-  
253 year-old children were able to plan at least one step ahead and that 5-year-olds would show  
254 superior planning abilities to 4-year-old children.

255 A further point that we address in this article is the effect of aging on planning abilities. In  
256 humans, there is a well-documented cognitive decline in executive functions (including planning)  
257 related to normal aging (e.g. Dempster, 1992; Hedden & Gabrieli, 2004; Salthouse, Atkinson, &  
258 Berish, 2003; West, 1996). Similarly, in rhesus macaques age-related cognitive impairments, in  
259 particularly a perseveration tendency and short-term memory deficits, have been found (Bartus,  
260 Fleming, & Johnson, 1978; Lai, Moss, Killiany, Rosene, & Herndon, 1995; Makris et al., 2007).  
261 As these behavioral changes seem to be rooted in a structural decline of the frontal lobe that is

262 present in different primate taxa (Bourgeois, Goldman-Rakic, & Rakic, 1994; Hedden & Gabrieli,  
263 2004), we hypothesized that planning abilities of great apes would decrease with age too.

264

## 265 Experiment 1

266

### 267 *Methods*

#### 268 *Subjects*

269 Two bonobos (*Pan paniscus*), seven chimpanzees (*Pan troglodytes*), one gorillas (*Gorilla*  
270 *gorilla*) and two orangutans (*Pongo abelii*) participated in this experiment. The subjects were  
271 housed at the Wolfgang Köhler Research Center, Leipzig Zoo (Leipzig, Germany). There were 8  
272 females and 4 males aged between 6 and 35 years ( $M_{\text{age}}$  17.0 years). Four subjects were  
273 nursery-reared and eight mother-reared (see Table 1 for detailed information on each subject).  
274 Subjects had participated in various cognitive tasks prior to the study. A study by Seed and  
275 colleagues (2009) is particularly relevant here. As in the current study the subjects also had to  
276 move a reward with their fingers either to the left or to the right while avoiding traps (that differed  
277 in appearance from the ones used in the present task). In contrast to the present study,  
278 however, there was no planning involved beyond the current decision. Only three of the seven  
279 chimpanzees of the current sample (Alex, Fifi, and Sandra) had participated in this prior study.  
280 Subjects lived in social groups of different sizes and had access to indoor (175–430 m<sup>2</sup>) and  
281 outdoor areas (1400–4000 m<sup>2</sup>). They were tested individually in special testing rooms (5.1–7.3  
282 m<sup>2</sup>). Subjects were not deprived of food and water was available *ad libitum* during testing.

283

284

285 *Materials*

286 The apparatus consisted of quadrangular box (height x length x depth: 47 x 67 cm x 5 cm) that  
287 was mounted to the wall of the enclosure (see Figure 1). Inside the box there was a vertical  
288 maze consisting of three horizontal levels that were made of grey PVC material. Open gaps  
289 (width: 3 cm) located in these levels allowed to pass the food reward that was placed in the  
290 maze on to the next lower levels. In total, there were 10 gaps located over three of the maze's  
291 levels. The gaps were distributed symmetrically, that is when our subjects moved the reward  
292 into a gap it fell always in between two gaps on the next level. On the first (uppermost) level,  
293 there were two gaps, on the second and third level, there were four gaps each. Furthermore,  
294 there was a vertical partition located in the middle of the apparatus between the second and  
295 third gap on the second and third level. Underneath each opening there were two transparent  
296 pieces of acrylic glass that channeled the food reward and a patch of rubber material glued to  
297 the apparatus to cushion the food reward when it fell from one level to the next. Both of these  
298 additional items served to prevent the food reward from skipping one level accidentally.

299 The front side of the apparatus (which was accessible to the apes) was made of transparent  
300 acrylic glass and contained three horizontal rows of ten slits each (height x width 1.8 x 5 cm;  
301 distance between the slits 1 cm) that allowed the apes to stick in their fingers and to move the  
302 food reward to the left and to the right on all three levels. The apes could extract the food  
303 reward from the apparatus via two large, circular holes on the lower side of the maze (diameter  
304 5.4 cm). Two ramps on the left and right of each hole ensured that the reward would roll behind  
305 one of the holes when the subjects passed the reward on from the third level to the bottom of  
306 the apparatus.

307 The experimenter could access the backside of the apparatus, made of transparent acrylic  
308 glass. It contained a circular opening in the middle of the uppermost level that we used for

309 baiting purposes. Furthermore, there were ten openings (height x length 3.0 x 4.5 cm)  
310 corresponding to the location of each of the maze's gaps. The experimenter inserted yellow  
311 traps through these openings to block the gaps and, thus, to prevent the passage of the reward.  
312 The subjects could visually inspect the yellow traps, made of stained, acrylic glass (height x  
313 length x depth 1.5 x 4 x 3.5 cm) when the experimenter inserted them in the apparatus. We  
314 used monkey chow pellets (height x length x depth 2.0 x 3.0 x 2.0 cm) as rewards. The pieces  
315 of monkey chow were solid and thick enough to prevent subjects from just pulling them through  
316 the slits in the front side of the apparatus.

317

### 318 *Procedure and Design*

319 In the beginning of each trial, the experimenter placed three traps into the apparatus in full view  
320 of the subjects so that they could visually assess the traps and their function (blockage of free  
321 passage). Then the experimenter introduced the reward into the apparatus via the baiting hole  
322 in the backside of the apparatus on the uppermost level. The trial ended when the subject had  
323 obtained the reward or had pushed it into a trap. When the subject had obtained the reward, we  
324 moved on to the next configuration. When the subject failed, the experimenter removed the  
325 trapped reward and dropped it into the food bucket. After 3-5 sec, the experimenter started the  
326 next trial by inserting another piece of food into the apparatus.

327 There were two rounds of 24 trial-unique trap configurations per subject (in total: 48  
328 configurations). We employed a maximum of 16 trials per configuration. When the subjects  
329 failed to obtain the reward after 16 trials with a given configuration, we skipped it and  
330 administered the next configuration. Each session consisted of a maximum of 16 trials or 3  
331 configurations (depending on which criterion was reached first).

332 There were two independent variables with regard to maze complexity: level of planning (LoP)  
333 and changes in direction (CiD). With regard to the LoP, the subject had to consider at the  
334 beginning of a given trial only the first (uppermost) level, the first and second (intermediate)  
335 level, or all three levels to obtain the reward. For each LoP, there were eight different  
336 configurations: in LoP 0, one trap was located in the uppermost level, the other two traps were  
337 either both in the second level or in the third level, either at position 1 and 4 or at position 2 and  
338 3 (for an example see Figure 2a). To solve such configurations the apes only had to take into  
339 account the traps at the current level, that is, the level where the reward was currently located.  
340 In LoP 1, two traps were blocking both openings on one side of the second level; the third trap  
341 was located on the other side either also in the second or in the third level (see Figure 2b).  
342 Hence, the apes could not solve this task by only taking into account the uppermost level in the  
343 beginning of a trial (as there were no traps in the uppermost level). Instead, they had to look one  
344 level ahead, that is, when making the first decision on the uppermost level the traps in the  
345 second level had to be considered. For LoP 2, two traps were placed in one side of the third  
346 level (i.e. this side was completely blocked), the third trap was on the other side, either also on  
347 the third or on the second level (see Figure 2c). Therefore, the apes had to consider the traps in  
348 the third level when the reward was still at the uppermost level when making the decision where  
349 to move the food reward. Hence, LoP was a measure of spatial distance of the task relevant  
350 items (i.e. the traps) from the starting point. The factor LoP allowed us to manipulate how many  
351 subgoals the subjects had to consider in order to make an informed first decision.

352 The second independent factor was number of changes in direction (CiD) that the subject had to  
353 perform to gain the reward after the first decision was made. In half of the 24 configurations,  
354 there was no change in direction necessary, that is, the apes either had to push the reward  
355 completely to the left or to the right to get the reward. In the other half of configurations, they  
356 had to change the direction of the reward once, that is, after deciding for the right or left side on

357 the uppermost level the apes had to change the direction of the reward in the second or third  
358 level to the other side. Thus, CiD can be considered as measure of path complexity by  
359 manipulating the degree of motor control required to solve the maze. The number of changes in  
360 direction was completely balanced across the different LoP configurations: for each LoP four  
361 configurations involved no change in direction (CiD 0) and four involved one change (CiD 1) in  
362 direction. The “correct” side of the maze was balanced across the 24 configurations. Finally, the  
363 order of configurations was pseudo-randomized with the restriction that no more than two  
364 configurations of the same LoP were presented in a row.

365

#### 366 *Scoring and analysis*

367 We videotaped all trials. We scored the following four dependent measures (see Table 2): (1)  
368 whether subjects obtained the reward in the first trial (T1) of a given configuration (T1 success,  
369 chance-level: 25% correct), (2) whether the first gap in the uppermost level into which they  
370 moved the reward in T1 was on the correct side for the final solution (T1 first decision, chance-  
371 level: 50% correct), (3) whether the first movement in T1 of the food reward on the uppermost  
372 level was directed towards the correct or incorrect side for the final solution (T1 first move,  
373 chance level: 50% correct), and (4) the number of trials per configuration the subjects needed to  
374 obtain the reward (chance-level: 4 trials). Moreover, we scored perseveration errors, that is, an  
375 error that was exactly the same error (level and position) incurred in the previous trial of the  
376 same configuration. In case the subjects failed within 16 trials we scored 17 trials for this  
377 configuration (i.e. the minimum number in which they could have solved the configuration). A  
378 second coder scored 20 % of the trials to assess interobserver reliability, which was excellent  
379 (T1 success:  $K = 1.0$ ,  $N = 113$ ,  $p < 0.001$ ; T1 first decision:  $K = 1.0$ ,  $N = 113$ ,  $p < 0.001$ ; T1 first move:  
380  $K = 0.93$ ,  $N = 113$ ,  $p < 0.001$ ; number of trials per configuration:  $r_s = 1.0$ ,  $N = 113$ ,  $p < 0.001$ ).



381 Subjects who performed above chance only with regard to the number of trials per configuration  
382 were indicative of significant post-error corrections. Above chance performance in T1 success  
383 was indicative of successful sequential decision making without necessarily taking into account  
384 upcoming levels. If the first decision was made completely randomly, subjects could still have  
385 obtained the reward in 50% of T1 trials (which was significantly above the chance level of 25%  
386 correct). Above chance performance in T1 first decision (in particular in LoP 1 and 2  
387 configurations) was indicative of planning, that is, upcoming levels were considered when the  
388 first decision was made. Finally, above chance level performance in T1 first move was indicative  
389 of whether planning was completed before the initial motor response was executed.

390 We applied Pearson's correlations to assess the relation between the T1 success performance  
391 and age. All p-values reported here are exact and two-tailed. Assumption of normality was met  
392 for the current data (Kolmogorov-Smirnov test:  $p > 0.05$ ). At the individual level, we used binomial  
393 tests for the binary variables T1 success and T1 first decision and the Wilcoxon signed rank test  
394 for the count variable number of trials per configuration to test against the chance level.

395 To test whether the dependent variables T1 success, T1 first decision, and number of trials per  
396 configuration were influenced by the factors level of planning (LoP), changes in direction (CiD),  
397 repetition of configurations, and the age of the subjects we used a Generalized Linear Mixed  
398 Model (GLMM; Baayen, 2008) into which we included these four predictors as covariates and  
399 subject as well as configuration identity as random effects. The models were fitted in R (R  
400 Development Core Team, 2011) using the function lmer of the R-package lme4 (Bates &  
401 Maechler, 2010). We assessed model stability by comparing the estimates derived by a model  
402 based on all data with those obtained from a model with subjects excluded one by one. The  
403 significance of the full model as compared to the null model (comprising only random effects;  
404 Forstmeier & Schielzeth, 2011) was established using a likelihood ratio test (Dobson, 2002).

405 Therefore, we used the R function `anova` with argument `test = "Chisq"`. All models reported  
406 here were found to be significant ( $p < 0.01$ ).

407 As the dependent variable 'number of trials' was a count response we used a poisson error  
408 distribution and the log link function. The response variables 'success in T1' and 'first decision in  
409 T1' were binary (success/failure), therefore, we specified binomial errors and the logit link  
410 function. We z-transformed all predictors to a mean of zero and a standard deviation of one to  
411 get comparable estimates. The intercepts of the models represented the sample mean assumed  
412 by the models. In the case of the logistic models, the fitted mean is revealed by the inverse logit-  
413 transformation of the intercept (i.e.  $\exp(\text{intercept}) / (1 + \exp(\text{intercept}))$ ). The corresponding P-value  
414 of the intercept indicates whether the intercept deviates significantly from the equal distribution  
415 which was the null hypothesis for the variable "first decision in T1" (proportion of correct  
416 decisions = 0.5). However, for the dependent variable "success in T1" the chance value was  
417 0.25. Therefore, we subtracted the logit-transformed chance-value from the estimate of the  
418 intercept and calculated the corresponding z- and P-value based on this adjusted estimate. In  
419 the case of the poisson model, the fitted mean is revealed by the inverse log-function  
420 ( $\exp(\text{intercept})$ ). As the chance value of the count variable "number of trials per configuration"  
421 was 4, we subtracted the log-transformed chance value from the estimate of the intercept and  
422 calculated the z- and P-value based on the adjusted estimate. However, since the dependent  
423 variables were not based on a simple linear function of the given predictor variables in the  
424 models, there was a minimal deviation of the sample mean assumed by the model from the  
425 actual sample mean. We corrected for this small deviation by adjusting the scaled variables by  
426 adding a constant value chosen such that the absolute difference between the actual sample  
427 mean and the fitted mean was minimized (the corresponding function was written by Roger  
428 Mundry, and is available upon request). Doing so did not affect any terms of the model except

429 for the intercept. Thereby, the intercept in these models became a reliable test of subjects'  
430 performance against chance while controlling for the covariates and random effects.

431

432

## Results

### 433 *Trial 1 Success with each Unique Maze Configuration*

434 Overall, subjects solved significantly more configurations in their first trial than expected by  
435 chance ( $40.3 \pm 5.6\%$  correct,  $z=3.46$ ,  $p<0.001$ ). Thus, subjects at the group level had learnt to  
436 avoid the traps. The GLMM indicates significant effects of CiD, repetition of configurations, and  
437 age on success in T1 (see Table 3): subjects performed better when no change in direction was  
438 necessary (CiD 0), improved in the second round compared to the first one, and younger  
439 subjects performed better than older ones. In line with that, subjects only scored above chance  
440 when no change in direction was required and in the second round (but not in the first one). The  
441 age effect on performance was supported by a significant correlation (Pearson correlation:  $r=-$   
442  $0.59$ ,  $n=12$ ,  $p<0.05$ ; see Figure 3 and Table 4). In contrast, there was no significant main effect  
443 of LoP. Across LoP, subjects solved more trials in T1 than expected by chance (see Table 3).

444 At an individual level, four chimpanzees and one bonobo performed significantly above chance  
445 ( $p<0.05$ ; see Table S1) and one further subject (an orangutan) performed above chance  
446 ( $p<0.05$ ) in the second round. These six subjects who learnt to avoid the traps ( $M_{\text{age}} 12.7 \pm 1.6$   
447 years) were on average much younger than the remaining five subjects ( $M_{\text{age}} 23.0 \pm 5.2$ ).

448 Thus, in contrast, to three older individuals ( $>20$  years of age) most of the younger apes at the  
449 individual level had learnt to avoid the traps as indicated by their significant above-chance  
450 performance in trial 1 of each unique maze configuration (see Table S1). In subsequent  
451 analyses we focused on these younger subjects ( $N=9$ ;  $<20$  years of age) to exclude the

452 confounding effect of older subjects that performed randomly even when they did not have to  
453 plan ahead on our measure of planning.

454

455 *First decision in trial 1 of each unique maze configuration*

456 Overall, the younger subjects (N=9) performed significantly better than expected by chance in  
457 their first decision in T1 ( $64.8 \pm 3.6$  % correct,  $z=4.07$ ,  $p<0.001$ ). Thus, subjects at the sub-group  
458 level considered the trap configuration when making their first decision at the uppermost level.  
459 The GLMM indicates no significant effects of age, LoP, CiD, or repetition (see Table 3).

460 Across the different LoPs, we found that the younger apes performed not only above chance in  
461 LoP 0 configurations but also in LoP 1 and LoP 2 (see Table 4, for an example see  
462 supplementary video 1) suggesting that the younger apes already considered two upcoming  
463 decisions before making the current one. Furthermore, the younger subjects performed above  
464 chance across CiD (see Table 4) suggesting that this measure of maze complexity was not a  
465 limiting factor for their first decision.

466 Considering the individual data we found that overall four subjects performed significantly above  
467 chance (three chimpanzees and one bonobo, all  $p<0.05$ ; see Table S2). Of these four subjects  
468 two scored significantly above chance in LoP 0, one in LoP 1, and two in LoP 2 configurations.

469

470 *First Move in trial 1 of each unique maze configuration*

471 When looking at the first move of the food reward of the younger apes we found that subjects  
472 performed above chance ( $63.2 \pm 4.5$  % correct,  $z=2.97$ ,  $p<0.05$ , see Table 4) indicating that the  
473 decision was made before the movement was executed.

474 *Number of trials per configuration to success*

475 Overall, the younger subjects did not perform different from the chance level of 4 trials ( $3.28 \pm$   
476  $0.46$  trials,  $z=-1.16$ ,  $p>0.1$ ). Therefore, we found no evidence for efficient post-error  
477 adjustments. This finding can be ascribed to the high rate of perseveration errors (i.e. the exact  
478 same error as in the previous trial): on average subjects made  $43.2 \pm 14.2$  perseveration errors.  
479 In 47.2 % of all error trials in which a perseveration error could occur (i.e. excluding the first trial  
480 of each configuration) subjects repeated the previously made error. The GLMM indicates  
481 significant effects of repetition of configurations (see Table 5): subjects needed more trials per  
482 configuration in the first round than in the second round. In contrast, there was no significant  
483 main effect of LoP, CiD or age.

484 At an individual level, five chimpanzees and one bonobo (that all were < 20 years old) solved  
485 the maze task in significantly less than 4 trials (all  $p<0.05$ , see Table S3). Two additional  
486 subjects, one bonobo and one orangutan, performed significantly better than chance in their  
487 second round ( $p<0.05$ ).

488

489 *Discussion*

490 Most of our younger subjects below the age of 20 years (four chimpanzees, one bonobo, and  
491 one orangutan) learnt to avoid the traps in contrast to the older ones. Importantly, these younger  
492 subjects considered not only the current level (LoP 0) when making the first decision. Instead,  
493 they took already the second and third level into account (LoP 1 and 2). This finding suggests  
494 that great apes below a certain age are able to plan their actions without extensive training up to  
495 two steps ahead. When errors occurred, however, the apes showed high levels of  
496 perseveration, that is, they had problems to adjust their behavior efficiently on a trial-to-trial  
497 basis.

498 The negative correlation between age and first trial performance suggests that, as predicted by  
499 studies on the age-related decline of executive functions in humans (Hedden & Gabrieli, 2004;  
500 Salthouse et al., 2003) and monkeys (Bartus et al., 1978; Lai et al., 1995; Makris et al., 2007),  
501 apes' planning abilities decrease with age. The only juvenile ape that failed to learn to avoid the  
502 traps was a female gorilla. Interestingly, gorillas were previously found to perform worst among  
503 the great apes in various inhibition tasks (Amici, Aureli, & Call, 2008). Though caution is  
504 required here as we have only tested a single gorilla, weak inhibitory control might underlie the  
505 juvenile gorilla's failure in the present task.

506 CiD but not LoP had a significant impact on the performance of our nonhuman subjects. CiD  
507 reflects the need to update the initially chosen direction on the second or third level of the maze  
508 (which often went along with a change of the hand used to move the reward). Updating the  
509 motor direction involves the inhibition of the previous response. LoP has also an inhibition  
510 component, that is, to suppress the action (first move) before a plan has been made. This type  
511 of inhibition, however, is different from changing the direction of the reward as it is not so much  
512 about the inhibition of previously used (prepotent) actions. The second important factor for LoP,  
513 however, seems the representation and updating of the plan (the sequence of subgoals towards  
514 to overarching goal) in working memory. The present data therefore suggest that nonhuman  
515 apes have difficulty in inhibiting previously used actions but not to plan and to represent a  
516 sequence of subgoals towards a goal.

517 With regard to the timing of apes' decision making process we were looking at the first move of  
518 the pellet on the uppermost level. Using a forward search or hill climbing strategy, the apes  
519 might have started to move the food reward randomly and still could have corrected the first  
520 move if necessary before the reward was moved into the first gap. But that was not what we  
521 found: some of the younger apes directed their first move of the reward to the correct side  
522 (across the different levels of planning). Thus, the decision involving the consideration of

523 upcoming levels was already made before the execution of the motor command. In other words,  
524 these apes planned before they acted.

525 Alternatively to the planning account, the apes might have rapidly learnt to make the first  
526 decision based on a fixed heuristic: avoid the side with two traps. Using such a rule would have  
527 yielded a perfect performance with the trap configurations used in Experiment 1. In order  
528 differentiate between a planning strategy and such a fixed heuristic, we conducted a follow-up  
529 experiment with two traps on each side.

530

531

## 532 Experiment 2

533 In Experiment 2, we examined whether those apes who learnt to avoid the traps in Experiment 1  
534 based their first decision on the heuristic: avoid the side of the apparatus with two traps. In  
535 Experiment 2, we inserted four traps in the apparatus, two on each side, to render this heuristic  
536 ineffective. We hypothesized that if the apes performed above chance in their first decision in T1  
537 the usage of this heuristic would be ruled out.

538 At the same time, the additional trap made the correct side (and therefore, the correct path)  
539 more complex as it contained two instead of just one trap. From a cognitive point of view, the  
540 apes might have used two different, though both valid strategies in Experiment 1: avoiding the  
541 blocked side (inference by exclusion) or planning of the correct path to follow (subgoaling). The  
542 comparison of Experiment 1 (3 traps) with Experiment 2 (4 traps) would allow us to draw a  
543 conclusion with regard to what kind of strategy the apes most likely used to solve the task: if  
544 their performance was negatively affected by the additional trap in the correct side of the maze,  
545 this would favor a subgoaling account.

546

547

*Methods*548 *Subjects*

549 The seven subjects who had passed Experiment 1 participated in this experiment. They  
550 included one bonobo, five chimpanzees, and one orangutan (see Table 1). There were 4  
551 females and 3 males aged between 6 and 18 years ( $M_{\text{age}}$  12.7 years). Two subjects were  
552 nursery-reared and five mother-reared.

553

554 *Materials*

555 The apparatus was identical to Experiment 1.

556

557 *Procedure and Design*

558 The procedure was identical to Experiment 1 with the exception that we inserted now four traps  
559 instead of three in the apparatus.

560 Like in Experiment 1, there were two rounds of 24 trial-unique configurations per subject (in  
561 total: 48 configurations). Per configuration we employed 16 trials at maximum. When the  
562 subjects failed to obtain the reward after 16 trials with a configuration we went on with the next  
563 configuration. Per session there was a maximum of 24 trials or 8 configurations (depending on  
564 which criterion was reached first). The order of presentations was pseudo-randomized with the  
565 restriction that no more than two configurations of the same LoP were presented in a row.

566 The additional trap did not affect the factor level of planning (LoP). Again, there were three LoPs  
567 (0-2) of eight configurations each. In contrast, the second independent variable, changes in



568 direction (CiD), was affected by the additional trap that was entered in the apparatus. Besides  
569 CiD 0 and 1 there were CiD 2 configurations in which the subject had to change the direction of  
570 the food reward after the first decision twice on the second and third level. For CiD 0 and 2,  
571 there were 6 configurations each, for CiD 1, there were 12 configurations. The number of  
572 changes in direction was completely balanced across the different LoPs: for each LoP, there  
573 were two CiD 0 and 2 configurations, respectively, and four CiD 1 configurations. Finally, the  
574 correct side of the apparatus was balanced across the 24 configurations.

575

#### 576 *Scoring and analysis*

577 Scoring and analyses were largely identical to Experiment 1. However, the chance levels  
578 differed in Experiment 2: number of trials per configuration had a chance level of 8 trials,  
579 considering T1 success chance was at 12.5 % correct. T1 first decision was not affected by the  
580 additional trap (chance level: 50 % correct).

581 We used the same GLMM as in Experiment 1. To compare their performance in T1 first decision  
582 between Experiment 1 and 2 we ran a combined GLMM with the data of the seven subjects that  
583 completed both Experiments. In this model we included the factors number of traps (i.e.  
584 Experiment 1 and 2), LoP, repetition of configurations, and age of subjects. CiD was not entered  
585 in this model as this factor was associated with the number of traps entered.

586

587

588

589

## Results

590

### 591 *Trial 1 Success with each Unique Maze Configuration*

592 Overall, subjects solved significantly more configurations in their first trial than expected by  
593 chance ( $49.4 \pm 4.8\%$ ,  $z=15.12$ ,  $p<0.001$ ) indicating that they avoided the traps at least at the  
594 current level. The GLMM indicates significant effects of LoP, CiD, and age on success in T1  
595 (see Table 6): subjects performed significantly better in LoP 0 ( $z=2.34$ ,  $p<0.05$ ) than in LoP 2  
596 configurations. There was no significant difference between LoP 0 and 1 ( $z=0.37$ ,  $p>0.5$ ) or  
597 between LoP 1 and 2 ( $z=1.94$ ,  $p=0.052$ ). Moreover, subjects performed better when no change  
598 in direction was required (CiD0) compared to one change (CiD 1,  $z=4.53$ ,  $p<0.001$ ) and two  
599 changes in direction (CiD 2,  $z=3.63$ ,  $p<0.001$ ). In contrast, there was no difference between CiD  
600 1 and CiD 2 ( $z=0.47$ ,  $p>0.5$ ). Finally, younger subjects performed better than older ones  
601 (Pearson correlation:  $r=-0.77$ ,  $n=7$ ,  $p<0.05$ ; see Figure 4). No significant effect was found for  
602 repetition of configurations. Across LoPs, CiDs, and repetitions subjects were above chance. At  
603 an individual level, all subjects were overall above chance (all  $p<0.01$ , see Table S4).

604

### 605 *First decision in trial 1 of each unique maze configuration*

606 Overall, the subjects made their first decision significantly more often to the correct side ( $57.7 \pm$   
607  $3.6\%$ ,  $z=2.75$ ,  $p<0.01$ ) than expected by chance, a finding that was already evident in the first  
608 round ( $57.7 \pm 3.9\%$ ,  $z=1.97$ ,  $p<0.05$ ). The GLMM indicates significant effects of CiD and age  
609 (see Table 6): subjects performed significantly better in the first decision in CiD 0 configurations  
610 compared to CiD 1 ( $z=3.34$ ,  $p<0.001$ ) or CiD 2 ( $z=2.75$ ,  $p<0.01$ ). In contrast, there was no  
611 difference between CiD 1 and 2 ( $z=0.27$ ,  $p>0.5$ ) configurations. In line with that, they only  
612 scored above chance in CiD 0 configurations but not in CiD 1 or 2 configurations. Finally,  
613 younger subjects performed better than older ones. No significant effect was found for LoP or

614 repetition of configurations. Subjects scored significantly above chance in LoP 0 and 1 but not in  
615 LoP 2 configurations. Thus, with four traps inserted in the apparatus we found evidence that the  
616 apes at the group level considered one (but not two) upcoming decisions when making the  
617 current one.

618 At the individual level, one chimpanzee performed significantly above chance ( $p < 0.01$ ), one  
619 further chimpanzee performed on a marginally significant level ( $p = 0.059$ ; see Table S5). Both of  
620 these subjects also tended to score above chance in LoP 0 and 1 configurations ( $p < .1$ ) but not  
621 in LoP 2 ( $p > 0.5$ ).

622 Comparing T1 first decision between Experiment 1 and 2, the GLMM reveals that their first  
623 decision was significantly worse when four rather than three traps were entered in the apparatus  
624 (see Table 7). The finding indicates that with two traps at each side of the apparatus the apes  
625 had more problems to make an informed first decision even though they still performed  
626 significantly above chance.

627

#### 628 *Number of trials per configuration to success*

629 Overall, subjects needed significantly fewer trials than the chance level (= 8 trials) per  
630 configuration ( $2.38 \pm 0.23$ ,  $z = 18.64$ ,  $p < 0.001$ ). The GLMM indicates significant effects of LoP,  
631 CiD, age, and repetition of configurations (see Table 8): subjects needed fewer trials in LoP 0  
632 ( $z = 2.46$ ,  $p < 0.05$ ) and LoP 1 ( $z = 1.99$ ,  $p < 0.05$ ) compared to LoP 2 configurations. In contrast,  
633 there was no difference between LoP 0 and 1 ( $z = 0.67$ ,  $p > 0.5$ ). Furthermore, subjects required  
634 fewer trials in CiD 0 configurations than in CiD 1 ( $z = 5.23$ ,  $p < 0.001$ ) and 2 ( $z = 5.00$ ,  $p < 0.001$ )  
635 configurations. In contrast, there was no difference between CiD 1 and 2 ( $z = -0.74$ ,  $p > 0.1$ ).  
636 Finally, younger subjects performed better than older ones and subjects performed significantly  
637 better in the second round than in the first round. Across LoP, CiD, and repetition of

638 configurations subjects performed above chance. At an individual level, all subjects performed  
639 above chance (all  $p < 0.01$ , see Table S6).

640

641 *Discussion*

642 At the group level, the seven great apes that in Experiment 1 succeeded in the first trial (with  
643 three traps entered in the apparatus) were also able to solve the four-trap version of the task.  
644 More specifically, they succeeded in the first trial more often and required fewer trials per  
645 configuration than expected by chance. Additionally, these apes also chose the correct side in  
646 their first decision of the first trial. In fact, they picked the correct side significantly above chance  
647 in LoP 0 and 1 configurations. Therefore, the heuristic “avoiding the side with two traps” seems  
648 not to be sufficient to explain the apes’ first decision. At the individual level, it became apparent  
649 that in particular the two youngest chimpanzees showed robust evidence for planning in the  
650 four-trap version of the current task.

651 Instead, the impact of CiD, i.e. the change in direction of the reward on the second and third  
652 level of the maze, on the first decision (that is made on the first level) highlights two issues.  
653 First, the apes took the subsequent levels into account when making the first decision. Second,  
654 only the least complex configurations (i.e., those not requiring a change in direction) were  
655 planned thoroughly by the subjects. In contrast, the same seven subjects were able in  
656 Experiment 1 to plan the correct path in CiD 1 configurations suggesting that the increased  
657 maze complexity (with four traps) is responsible for their failure in CiD 1 and 2 configurations of  
658 Experiment 2.

659 Having ruled out the heuristic based on the number of traps on each side, a comparison  
660 between Experiment 1 and 2 is particularly informative with regard to the strategy used:  
661 inference by exclusion or planning. Recall that in Experiment 1 subjects could have used two

662 cognitive strategies to guide their first decision: either to avoid the side that was completely  
663 blocked (inference by exclusion), or to plan the path through the maze focusing also on the  
664 configuration of the correct side (subgoaling). In line with the subgoaling account, we found that  
665 the first decision was significantly worse in Experiment 2 compared to Experiment 1. Together  
666 with the impact of CiD on the T1 first decision performance, this finding suggests that the  
667 complexity of the correct path was a limiting factor for the ape's performance in Experiment 2  
668 and that they were engaging in a subgoaling strategy when making the first decision.

669

670

### Experiment 3

671 Once we had established the strategy that apes used to solve the task and the impact of age on  
672 their performance, we presented 4- and 5-year-old human preschoolers with the same paradigm  
673 as the nonhuman apes in Experiment 1. Specifically, we were interested in whether the  
674 children's performance would be affected by the same factors.

675

676

### *Methods*

#### *Subjects*

678 Fifteen 4-year-old and 12 5-year-old children recruited from seven different kindergartens in  
679 Leipzig, Germany participated in this experiment. These children were drawn from the  
680 participant database of the Max Planck Institute for Evolutionary Anthropology. As three children  
681 refused to be tested before all configurations could be completed our final sample consisted of  
682 12 4-year-olds and 12 5-year-olds that completed all trials (4-year-olds:  $M_{\text{age}} 47.4 \pm 0.6$  months,  
683 50 % females; 5-year-olds:  $M_{\text{age}} 59.5 \pm 0.7$  months, 50 % females). The excluded subjects  
684 performed on similar levels as the subjects of the same age that were included in the final  
685 sample.

686

#### *Materials*

688 The apparatus used in Experiment 3 was identical in construction to the one used with the  
689 nonhuman apes. The only difference was that the levels of the maze were made of wood

690 (instead of PVC). Moreover, the apparatus had a base-plate to keep it upright when it was  
691 placed on a table.

692

### 693 *Procedure and Design*

694 The procedure was similar to the nonhuman apes tested in Experiment 1. We administered two  
695 rounds of 24 trial-unique configurations. However, the children received eight trials per  
696 configuration at maximum (instead of 16). Per session there was a maximum of 48 trials or 24  
697 configurations (depending on which criterion was reached first).

698 The reward for the children consisted of a toy that varied from trial to trial (stickers, marbles,  
699 balloons, etc.). This reward was put in a bottle cap and wrapped in aluminum foil before the  
700 child entered the test room. The cap prevented the children to remove the reward directly  
701 through the slits in the front side of the apparatus. The subjects could not see what was inside  
702 the cap before they extracted the reward from the apparatus and removed the aluminum foil.

703 Subjects received only minimal verbal instruction at the beginning of each session. The  
704 standardized instruction was that the apparatus was a “gift machine”. The experimenter  
705 instructed the child that she was allowed to put her finger through all the slits in the front side of  
706 the apparatus and that there were two big holes at the bottom of the apparatus. Then the  
707 experimenter told the child that there were surprises that she could gain. The experimenter  
708 entered the traps in the apparatus in full view of the child and placed the first “surprise” inside  
709 the apparatus and prompted the child: “This surprise is for you. Go, get it out!” No instructions  
710 were given with regard how to remove the item from the apparatus or to the function of the  
711 traps.

712

713 *Scoring and analysis*

714 Same as in Experiment 1. A second coder scored 20 % of the trials to assess interobserver  
715 reliability, which was excellent (T1 success:  $K=0.97$ ,  $N=240$ ,  $p<0.001$ ; T1 first decision:  $K=1.0$ ,  
716  $N=240$ ,  $p<0.001$ ; T1 first move:  $K=0.93$ ,  $N=240$ ,  $p<0.001$ ; number of trials per configuration:  
717  $r_s=0.95$ ,  $N=240$ ,  $p<0.001$ ).

718 In addition, to compare the motor control performance of children with the younger nonhuman  
719 apes (Exp. 1) we conducted a repeated measures ANOVA with the dependent measure  
720 'success in T1' and the factors CiD and our three subject groups (younger nonhuman apes, 4-  
721 year-old children, and 5-year-old children). Moreover, to compare apes' and children's planning  
722 abilities we conducted another repeated measures ANOVA with the dependent measure 'first  
723 decision in T1' and the factors LoP and our three subject groups. Post-hoc pairwise  
724 comparisons (all p-values were Bonferroni corrected) were conducted on the basis of significant  
725 interactions.

726

727 *Results*

728 *Trial 1 Success with each Unique Maze Configuration*

729 Overall, subjects solved significantly more configurations in their first trial than expected by  
730 chance ( $68.0 \pm 2.6\%$  correct,  $z=3.58$ ,  $p<0.001$ ). The GLMM indicates significant effects of LoP,  
731 repetition of configurations, and age on Trial 1 success (see Table 9): subjects performed better  
732 in LoP 0 than in LoP 1 ( $z=5.41$ ,  $p<0.001$ ) and LoP 2 configurations ( $z=5.43$ ,  $p<0.001$ ) and they  
733 were better in LoP 1 compared to LoP 2 configurations ( $z=2.41$ ,  $p<0.05$ ). Moreover, subjects  
734 improved in the second round compared to the first one, and 5-year-olds performed better than  
735 4-year-olds. Four- and 5-year-olds performed above chance across LoP (all  $p<.01$ ). In contrast,



736 there was no significant main effect of CiD. Across CiD, subjects solved more trials in T1 than  
737 expected by chance (see Table 9). At an individual level, all 4- and 5-year-olds performed  
738 overall above chance ( $p < 0.01$ ; see Table S7).

739

740 *First decision in trial 1 of each unique maze configuration*

741 Overall, subjects performed better than expected by chance in their first decision in T1 ( $72.6 \pm$   
742  $2.2$  % correct,  $z = 3.19$ ,  $p = 0.001$ ). The GLMM indicates a significant effect of LoP, repetition, and  
743 age (see Table 9): subjects performed better in LoP 0 than in LoP 1 ( $z = 4.93$ ,  $p < 0.001$ ) and LoP  
744 2 configurations ( $z = 5.57$ ,  $p < 0.001$ ) and they were better in LoP 1 compared to LoP 2  
745 configurations ( $z = 2.74$ ,  $p < 0.01$ ). Moreover, subjects improved in the second round compared to  
746 the first one, and 5-year-olds performed better than 4-year-olds. However, at the group level  
747 both 4- and 5-year-olds only performed above chance in LoP 0 and 1 configurations but not in  
748 LoP 2 configurations (see Table 10). CiD did not have a significant effect on their performance.  
749 Across CiD, subjects solved more trials in T1 than expected by chance (see Table 10).

750 Considering the individual data we found that eight of twelve 4-year-olds and ten of twelve 5-  
751 year-olds performed overall significantly above chance (all  $p < 0.05$ ; see Table S8). Of these  
752 eight 4-year-olds all scored significantly above chance in LoP 0, one in LoP 1, and none in LoP  
753 2 configurations. All ten 5-year-olds scored significantly above chance in LoP 0, seven in LoP 1,  
754 and one in LoP 2 configurations.

755

756 *First Move in trial 1 of each unique maze configuration*

757 When looking at the first move of the reward in the beginning of T1 we found that overall both 4-  
758 year-olds ( $60.1 \pm 2.6$  % correct,  $z = 2.54$ ,  $p < 0.05$ ) and 5-year-olds ( $71.4 \pm 2.8$  % correct,  $z = 6.19$ ,

759  $p < 0.001$ ) performed above chance indicating that subjects decided before the movement was  
760 executed.

761

#### 762 *Number of trials per configuration to success*

763 Overall, subjects required significantly fewer trials than expected by chance ( $1.56 \pm 0.07$  trials,  
764  $z = 20.94$ ,  $p < 0.001$ ). With regard to perseveration errors, subjects made on average  $8.0 \pm 1.9$  (4-  
765 year-olds:  $10.3 \pm 3.1$ , 5-year-olds:  $5.8 \pm 2.2$ ) repetition errors. In 45.6 % of all error trials in  
766 which a perseveration error could occur (i.e. excluding the first trial of each configuration)  
767 subjects repeated the previously made error. The GLMM indicates significant effects of LoP,  
768 repetition of configurations, and age on success in T1 (see Table 11): subjects tended to  
769 perform better in LoP 0 than in LoP 1 ( $z = 1.85$ ,  $p = 0.065$ ) and LoP 2 configurations ( $z = 3.00$ ,  
770  $p < 0.01$ ) and they tended to perform better in LoP 1 compared to LoP 2 configurations ( $z = 1.87$ ,  
771  $p = 0.062$ ). Moreover, subjects improved in the second round compared to the first one, and 5-  
772 year-olds performed better than 4-year-olds. Four- and 5-year-olds performed above chance  
773 across LoP (all  $p < 0.001$ ). In contrast, there was no significant main effect of CiD. Across CiD,  
774 subjects required fewer trials than expected by chance (see Table 11). At an individual level, all  
775 4- and 5-year-olds performed overall above chance ( $p < 0.001$ ; see Table S9).

776

#### 777 *Comparison between younger non-human apes and children*

778 With regard to success in T1 a repeated measures ANOVA revealed a significant main effect of  
779 group ( $F[2,30] = 10.58$ ;  $p < 0.001$ ), CiD ( $F[1,30] = 7.64$ ;  $p < 0.05$ ), and group x CiD interaction  
780 ( $F[2,30] = 3.48$ ;  $p < 0.05$ ). Post-hoc pairwise comparisons showed that 4-year olds performed better  
781 than apes only when a change in direction was required (CiD 1,  $p < 0.05$ ; CiD 0,  $p > 0.5$ ; see also

782 Figure 5). Five-year-olds performed better than the apes irrespective of CiD (CiD 0,  $p < 0.05$ ; CiD  
783 1,  $p < 0.001$ ). Finally, the performance of 4- and 5-year olds did not differ significantly irrespective  
784 of CiD (CiD 0,  $p > 0.1$ , CiD 1,  $p > 0.1$ ).

785 With regard to the first decision in T1 a repeated measures ANOVA revealed a significant a  
786 significant main effect of group ( $F[2,30]=4.04$ ;  $p < .05$ ), LoP ( $F[2,60]=37.16$ ;  $p < .001$ ), and a group  
787 x LoP interaction ( $F[4,60]=4.99$ ;  $p < .01$ ). Post-hoc tests revealed that 4-year olds performed  
788 better than apes in LoP 0 ( $p < 0.01$ ) but not in LoP 1 ( $p > 0.5$ ) or LoP 2 ( $p > 0.5$ ; see Figure 6). Five-  
789 year-olds performed better than the apes in LoP 0 ( $p < 0.001$ ) and LoP 1 ( $p < 0.05$ ) but not in LoP  
790 2 ( $p > 0.5$ ). Finally, 5-year olds performed better than 4-year-olds only in LoP 1 ( $p < 0.05$ ) but not  
791 in LoP 0 ( $p > 0.1$ ) or LoP 2 ( $p > 0.5$ ).

792

793

### *Discussion*

794 Four- and 5-year-old preschoolers quickly learnt to avoid the traps without any prior training or  
795 instruction with regard to the function of the traps. Overall, the children made only few  
796 perseveration errors indicating that for the most part children adjusted their behavior flexibly  
797 when errors occurred. When one of the few errors occurred, however, the errors were made  
798 due to a perseveration bias in almost half of the cases.

799 In line with our hypothesis, 5-year-olds performed better than 4-year-olds. Crucially, when  
800 making the first decision, the 4- and 5-year-old children did not only consider the current level  
801 (LoP 0) but also the next level (LoP 1). However, at the group level both, the 4- and 5-year-olds  
802 failed to consider traps located two levels ahead (LoP 2), At the individual level it became clear  
803 that all 4-year-olds except for one did not plan their moves reliably at all whereas most of the 5-  
804 year-olds considered at least one level beyond the current level and one individual even two  
805 levels. This finding suggests that 4-year-old children in the current task planned their actions at

806 maximum one step ahead while the 5-year-olds more reliably planned their actions and were  
807 able to plan their moves up to two steps ahead. In contrast to the younger nonhuman apes  
808 (Exp. 1), the children showed no drop in performance when a change in direction was required.  
809 Moreover, the children outperformed the younger apes in their first decision in LoP 0. In LoP 1,  
810 however, only the 5-year olds performed better than the younger apes and differences between  
811 groups disappeared in LoP 2.

812 The difference in planning abilities of 4- and 5-year-old children reported here fits well with  
813 previous research showing an increase in planning abilities between four and five years of age  
814 across different experimental paradigms (Fabricius, 1988; Klahr & Robinson, 1981; Wellman et  
815 al., 1984, 1985). Wellman and colleagues (1985) noted that planning (compared to perceptual  
816 strategies such as sighting) becomes the dominant search strategy over the preschool years. In  
817 line with that, 4-year-olds were previously found to exhibit a mixture between sighting and  
818 planning (Fabricius, 1988) and were found to plan consistently only one choice ahead beyond  
819 the current one (Klahr & Robinson, 1981; Wellman et al., 1984). Five-year-olds were shown to  
820 consider alternatives in a route planning task (Fabricius, 1988) and most of them were found to  
821 be able to plan between two and four steps ahead in a variant of the Tower of Hanoi task (Klahr  
822 & Robinson, 1981). The current data provide an independent confirmation of these findings with  
823 4-year-olds exhibiting a limit to plan only one step ahead while 5-year-olds planned their moves  
824 more reliably and at least one 5-year-old was able to plan two steps ahead. Importantly, the  
825 accordance of the results of the current paradigm with established planning tasks such as route  
826 planning tasks or the Tower of Hanoi provides evidence for the validity of the current  
827 experimental setup.

828 With regard to the predictors of the children's performance we found that LoP but not CiD had a  
829 significant impact across the different response variables. Even the 5-year-olds' performance  
830 markedly decreased from LoP 0 (91 % correct) to LoP 2 (60 %) indicating that planning ahead

831 in the currently used setting was not a trivial undertaking for them. Interestingly, the  
832 preschoolers' performance was not affected by CiD, that is, they had no problems to update the  
833 direction of the reward on the second or third level. This indicates that (lack of) response  
834 inhibition alone seems not to be sufficient to explain their weak performance in LoP 2  
835 configurations. LoP describes the length of the sequence of subgoals that are to be considered  
836 when making the first decision. Therefore, the representation and updating of a sequence of  
837 more than one subgoal in working memory seems to be the limiting factor for the preschoolers'  
838 performance.

839 Over the preschool years inhibitory control, cognitive flexibility, working memory retention  
840 capacity and updating enhances (Diamond, 2006; Garon, Bryson, & Smith, 2008). Espy and  
841 Bull (2005) related working memory capacity of 3 to 6-year-old preschoolers to attentional  
842 control (while controlling for age). In contrast, response inhibition was not found to be related to  
843 working memory capacity. Accordingly, higher working memory capacity allowed preschoolers  
844 to maintain task-relevant information in an active state. Attentional control also plays a crucial  
845 role in the present task. With increasing levels of planning the subjects need to shift their  
846 attention across a sequence of subgoals to make an informed first decision. Such cognitive  
847 flexibility (also referred to as shifting) has also been related in preschoolers (Bull, Espy, & Senn,  
848 2004) to one of the standard planning tasks, the Tower of Hanoi. In line with that, the present  
849 results suggest that shifting attention between two or more subgoals is critical for children's  
850 planning performance

851

852

853

## General Discussion

854 Comparing the performance of nonhuman great apes and human preschool children in the  
855 present maze task suggests that 4- and 5-year-olds were superior to the apes with regard to  
856 avoiding the traps when no planning was necessary and post-error trial-to-trial adjustments in  
857 behavior. This was indicated by a better performance in T1 success and number of trials per  
858 configurations of the children compared to the apes. However, when focusing on our measure  
859 of planning (T1 first decision: LoP 1 and 2) we found that younger nonhuman apes did perform  
860 at similar levels as human preschoolers. In contrast to the 4-year olds, two younger nonhuman  
861 apes and one 5-year-old preschooler were able to plan two steps ahead.

862 In line with previous research, only 5-year-old human children were shown to be able to plan  
863 more than one step ahead which is the key for the development of a problem-reduction or  
864 subgoaling strategy. Importantly, we extend the usage of such subgoaling abilities here to  
865 nonhuman apes. Contrary to previous research using different, training-dependent paradigms,  
866 we show that also nonhuman apes (below the age of 20) are able to plan more than one step  
867 ahead. As shown in Experiment 2, this performance could not be solely attributed to a fixed  
868 heuristic or perceptual strategy such as sighting. Rather, the predetermination of the correct  
869 path before the first move of the reward on the uppermost level is indicative of a subgoaling  
870 strategy.

871 One might argue that the comparison between nonhuman apes and human children is  
872 confounded by some differences in the experimental procedure: the children got only eight  
873 instead of 16 trials per configuration and they completed up to 48 instead of 16 trials per day.  
874 However, the younger nonhuman apes and the children only very rarely received eight or more  
875 trials per configuration. Therefore, the maximum number of trials per configuration is unlikely to

876 have a strong impact on the differences between the samples. The different number of sessions  
877 between the groups might indeed have affected the learning speed. However, when looking at  
878 the effect of order of configurations and repetition we found that both samples improved with  
879 regard to the number of trials per configuration and success in T1 across the two rounds of 24  
880 configurations. The children improved also with regard to the first decision in T1 between round  
881 1 and 2. The nonhuman apes, in contrast, did not improve in their first decision in T1 between or  
882 within the two rounds. Therefore, the finding that some of the younger nonhuman apes, unlike  
883 4-year-old children, performed significantly above chance in LoP 2 configurations is unlikely due  
884 to a difference in the number of sessions received.

885 Despite these similarities in the extent of planning, detailed analyses of nonhuman apes and  
886 human preschoolers' performance also revealed intriguing differences in their cognitive  
887 limitations: whereas the great apes' performance was largely influenced by CiD, a measure of  
888 response inhibition, human children's performance was not affected by this factor. Instead,  
889 children's performance was mainly affected by LoP, a measure of the number of subgoals to be  
890 considered towards the overarching goal. Poor response inhibition is also a likely candidate for  
891 great apes' failure to adjust their performance on a trial-to-trial basis and to avoid traps located  
892 in the current level as response inhibition is essential to overcome perseveratory tendencies.  
893 Thus, the present results suggest that great apes' performance in the current task was limited  
894 by deficits in response inhibition whereas children had problems to control and shift their  
895 attention between subgoals. In line with that, previous research indicated that cognitive flexibility  
896 (shifting) exhibits a slower developmental trajectory than inhibition and working memory in  
897 human children (Davidson, Amso, Anderson, & Diamond, 2006).

898 With regard to the nonhuman apes, response inhibition as limiting factor for their problem-  
899 solving skills is also in line with previous studies: evidence from reverse contingency task  
900 (Boysen & Berntson, 1995; Boysen, Berntson, & Mukobi, 2001; Vlamings, Uher, & Call, 2006)

901 and the detour-reaching task (Vlamings, Hare, & Call, 2010) revealed considerable deficits in  
902 the inhibition of prepotent responses in great apes. However, note that in the latter study 4- and  
903 5-year-old children performed actually on similar levels to bonobos and chimpanzees but worse  
904 than orangutans. Also in trap tasks like the trap-tube task great apes showed serious difficulties  
905 to overcome their bias to move the reward towards their own body (Limongelli, Boysen, &  
906 Visalberghi, 1995; Povinelli, 2000). When they were allowed to rake the reward instead pushing  
907 it away from their body their performance increased dramatically (Martin-Ordas, Call, &  
908 Colmenares, 2008; Mulcahy & Call, 2006).

909 In contrast to this shortage of response inhibition, working memory capacity and updating has  
910 been found to be excellent in nonhuman apes: the numerical ordering task revealed that  
911 chimpanzees can quickly store and update up to seven items in short-term memory with the  
912 highest performance achieved by a 7-year-old chimpanzee (Inoue & Matsuzawa, 2007; Kawai &  
913 Matsuzawa, 2000). Taking together, previous research supports the characterization of great  
914 apes executive functions as indicated by the present data: weak response inhibition but high  
915 working memory performance.

916 The current findings have implications for the evolution of executive functions and physical  
917 cognition: as shown by Herrmann and colleagues (2007) 2.5-year-old children exhibit similar  
918 cognitive skills as chimpanzees in the physical domain (including the scales measuring their  
919 understanding of space, quantities, and causality). The current study adds planning in the  
920 physical domain to this comparison. And again the nonhuman apes are found to perform at high  
921 levels compared to human children. Executive functions and the structure of the prefrontal  
922 cortex mature late in development in humans (Benes, 2001; Gogtay et al., 2004). This might  
923 explain why juvenile and young adult great apes even outperform 4-year-old human children in  
924 their planning abilities. Also, the age-related cognitive decline of planning abilities in nonhuman  
925 apes reported here match the findings of the human cognitive aging literature (e.g., Salthouse et



926 al., 2003; West, 1996). All of these findings are in line with a common underlying neural basis of  
927 great apes' planning abilities in the prefrontal cortex. Thus, the sophisticated executive functions  
928 that allow the planning of multi-step activities appear to be a conserved trait across the evolution  
929 of great apes. In contrast, we found across all four species of nonhuman great apes deficits in  
930 motor control compared to 4- and 5-year-old human preschoolers. Interestingly, enhanced  
931 manual motor control has been proposed to be the common starting point for the evolution of  
932 hominin tool making and language (Ambrose, 2001). There is even a shared neural substrate  
933 (Broca's area) of speech development and manual motor control (including tool use) during the  
934 first two years of human ontogeny (Greenfield, 1991). After the first two years, however, cortical  
935 differentiation is thought to lead to a more autonomous neural processing of speech and manual  
936 motor control. Therefore, the better performance of 4- and 5-year-old preschoolers in motor  
937 control compared to nonhuman apes might be based on an adaptation for tool use and /or  
938 language in the hominin lineage.

939 In summary, the present study provides compelling evidence for the usage of a subgoaling  
940 strategy involving the planning of a sequence of at least two subgoals in nonhuman apes.  
941 Younger apes below the age of 20 years showed planning abilities that were on a par with 5-  
942 year-old human children. The cognitive limitations in this planning task, however, differed  
943 between humans and nonhumans: whereas all nonhuman ape species exhibited deficits in  
944 motor inhibition the human preschoolers showed difficulties in attentional control. This finding  
945 supports the notion that a major change in the human evolution has been to optimize motor  
946 control with its implications for language and tool-use (Greenfield, 1991). As in human children  
947 specialized skills for social cognition have been reported, future directions of this research may  
948 be to examine whether great apes planning abilities in the physical domain also extend to the  
949 social world.

950

951

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957

958 Conflict of interest

959 The authors declare that they have no conflict of interest.

960

## References

- 961 Ambrose, S. H. (2001). Paleolithic technology and human evolution. *Science*, 291(5509), 1748-1753.
- 962 Amici, F., Aureli, F., & Call, J. (2008). Fission-fusion dynamics, behavioral flexibility, and inhibitory control  
963 in primates. *Current Biology*, 18(18), 1415-1419.
- 964 Baayen, R. H. (2008). *Analyzing linguistic data: A practical introduction to statistics using R*: Cambridge  
965 University Press.
- 966 Bard, K. A. (1995). Sensorimotor cognition in young feral orangutans (*Pongo pygmaeus*). *Primates*, 36(3),  
967 297-321.
- 968 Bartus, R. T., Fleming, D., & Johnson, H. (1978). Aging in the rhesus monkey: Debilitating effects on  
969 short-term memory. *Journal of Gerontology*, 33(6), 858-871.
- 970 Bates, D., & Maechler, M. (2010). lme4: Linear mixed-effects models using S4 classes. R package version  
971 0.999375-35. 2010. URL <http://CRAN.R-project.org/package=lme4>.
- 972 Benes, F. M. (2001). The development of prefrontal cortex: The maturation of neurotransmitter systems  
973 and their interactions. *Handbook of developmental cognitive neuroscience*, 79-92.
- 974 Beran, M. J., & Parrish, A. E. (2012). Sequential responding and planning in capuchin monkeys (*Cebus*  
975 *apella*). *Animal Cognition*, 15(6), 1085-1094.
- 976 Beran, M. J., Pate, J. L., Washburn, D. A., & Rumbaugh, D. M. (2004). Sequential responding and planning  
977 in chimpanzees (*Pan troglodytes*) and rhesus macaques (*Macaca mulatta*). *Journal of*  
978 *Experimental Psychology: Animal Behavior Processes*; *Journal of Experimental Psychology:*  
979 *Animal Behavior Processes*, 30(3), 203.
- 980 Bingham, H. C. (1929). *Selective transportation by chimpanzees*: Johns Hopkins Press.
- 981 Biro, D., & Matsuzawa, T. (1999). Numerical ordering in a chimpanzee (*Pan troglodytes*): Planning,  
982 executing, and monitoring. *Journal of Comparative Psychology*, 113(2), 178-185.
- 983 Bourgeois, J. P., Goldman-Rakic, P. S., & Rakic, P. (1994). Synaptogenesis in the prefrontal cortex of  
984 rhesus monkeys. *Cerebral Cortex*, 4(1), 78-96.
- 985 Boysen, S. T., & Berntson, G. G. (1995). Responses to quantity: Perceptual versus cognitive mechanisms  
986 in chimpanzees (*Pan troglodytes*). *Journal of Experimental Psychology: Animal Behavior*  
987 *Processes*, 21(1), 82-86.
- 988 Boysen, S. T., Berntson, G. G., & Mukobi, K. L. (2001). Size matters: Impact of item size and quantity on  
989 array choice by chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology*,  
990 115(1), 106.
- 991 Bull, R., Espy, K. A., & Senn, T. E. (2004). A comparison of performance on the Towers of London and  
992 Hanoi in young children. *Journal of Child Psychology and Psychiatry*, 45(4), 743-754.
- 993 Charness, N. (1981). Search in chess: Age and skill differences. *Journal of Experimental Psychology:*  
994 *Human Perception and Performance*, 7(2), 467.
- 995 Cramer, A. E. (1995). *Computations on metric cognitive maps: how vervet monkeys solve the traveling*  
996 *salesman problem*: UCLA.
- 997 Davidson, M. C., Amso, D., Anderson, L. C., & Diamond, A. (2006). Development of cognitive control and  
998 executive functions from 4 to 13 years: Evidence from manipulations of memory, inhibition, and  
999 task switching. *Neuropsychologia*, 44(11), 2037.
- 1000 Dempster, F. N. (1992). The rise and fall of the inhibitory mechanism: Toward a unified theory of  
1001 cognitive development and aging. *Developmental Review*, 12(1), 45-75.
- 1002 Diamond, A. (2006). The early development of executive functions. *Lifespan cognition: Mechanisms of*  
1003 *change*, 70-95.
- 1004 Dobson, A. J. (2002). *An introduction to generalized linear models*. Boca Raton: Chapman & Hall/CRC  
1005 press.

- 1006 Epstein, R., Kirshnit, C., & Lanza, R. (1984). "Insight" in the pigeon: Antecedents and determinants of an  
1007 intelligent performance. *Nature*, 308, 61-62.
- 1008 Espy, K. A., & Bull, R. (2005). Inhibitory processes in young children and individual variation in short-term  
1009 memory. *Developmental Neuropsychology*, 28(2), 669-688.
- 1010 Fabricius, W. V. (1988). The development of forward search planning in preschoolers. *Child*  
1011 *Development*, 59, 1473-1488.
- 1012 Forstmeier, W., & Schielzeth, H. (2011). Cryptic multiple hypotheses testing in linear models:  
1013 overestimated effect sizes and the winner's curse. *Behavioral Ecology and Sociobiology*, 65(1),  
1014 47-55.
- 1015 Frigaszy, D., Johnson-Pynn, J., Hirsh, E., & Brakke, K. (2003). Strategic navigation of two-dimensional  
1016 alley mazes: comparing capuchin monkeys and chimpanzees. *Animal Cognition*, 6(3), 149-160.
- 1017 Frigaszy, D., Kennedy, E., Murnane, A., Menzel, C., Brewer, G., Johnson-Pynn, J., & Hopkins, W. (2009).  
1018 Navigating two-dimensional mazes: chimpanzees (*Pan troglodytes*) and capuchins (*Cebus apella*  
1019 sp.) profit from experience differently. *Animal Cognition*, 12(3), 491-504.
- 1020 Fuster, J. M. (2002). Frontal lobe and cognitive development. *Journal of Neurocytology*, 31(3), 373-385.
- 1021 Gallistel, C., & Cramer, A. E. (1996). Computations on metric maps in mammals: getting oriented and  
1022 choosing a multi-destination route. *Journal of Experimental Biology*, 199(1), 211-217.
- 1023 Gardner, W., & Rogoff, B. (1990). Children's deliberateness of planning according to task circumstances.  
1024 *Developmental Psychology*, 26(3), 480.
- 1025 Garon, N., Bryson, S. E., & Smith, I. M. (2008). Executive function in preschoolers: A review using an  
1026 integrative framework. *Psychological Bulletin*, 134(1), 31.
- 1027 Gogtay, N., Giedd, J. N., Lusk, L., Hayashi, K. M., Greenstein, D., Vaituzis, A. C., . . . Toga, A. W. (2004).  
1028 Dynamic mapping of human cortical development during childhood through early adulthood.  
1029 *Proceedings of the National Academy of Sciences of the United States of America*, 101(21), 8174-  
1030 8179.
- 1031 Goldman-Rakic, P. S. (1987). Circuitry of primate prefrontal cortex and regulation of behavior by  
1032 representational memory. *Comprehensive Physiology*.
- 1033 Greenfield, P. M. (1991). Language, tools and brain: The ontogeny and phylogeny of hierarchically  
1034 organized sequential behavior. *Behavioral and Brain Sciences*, 14(4), 531-551.
- 1035 Hayes-Roth, B., & Hayes-Roth, F. (1979). A cognitive model of planning. *Cognitive Science*, 3(4), 275-310.
- 1036 Hedden, T., & Gabrieli, J. D. E. (2004). Insights into the ageing mind: a view from cognitive neuroscience.  
1037 *Nature Reviews Neuroscience*, 5(2), 87-96.
- 1038 Herrmann, E., Call, J., Hernández-Lloreda, M. V., Hare, B., & Tomasello, M. (2007). Humans have evolved  
1039 specialized skills of social cognition: The cultural intelligence hypothesis. *Science*, 317(5843),  
1040 1360-1366.
- 1041 Inoue, S., & Matsuzawa, T. (2007). Working memory of numerals in chimpanzees. *Current Biology*,  
1042 17(23), R1004-R1005.
- 1043 Inoue, S., & Matsuzawa, T. (2009). Acquisition and memory of sequence order in young and adult  
1044 chimpanzees (*Pan troglodytes*). *Animal Cognition*, 12(1), 59-69.
- 1045 Iversen, I. H., & Matsuzawa, T. (2001). Acquisition of navigation by chimpanzees (*Pan troglodytes*) in an  
1046 automated fingermaze task. *Animal Cognition*, 4(3), 179-192.
- 1047 Janson, C. (2013). Death of the (traveling) salesman: Primates do not show clear evidence of multi-step  
1048 route planning. *American Journal of Primatology*(9999), 1-11. doi: DOI: 10.1002/ajp.22186
- 1049 Kawai, N., & Matsuzawa, T. (2000). Numerical memory span in a chimpanzee. *Nature*, 403, 39.
- 1050 Kimberg, D. Y., & Farah, M. J. (1993). A unified account of cognitive impairments following frontal lobe  
1051 damage: The role of working memory in complex, organized behavior. *Journal of Experimental*  
1052 *Psychology: General*, 122(4), 411.

- 1053 Klahr, D. (1994). Discovering the present by predicting the future. In M. Haith, J. Benson, R. J. Roberts &  
 1054 B. Pennington (Eds.), *The development of future-oriented processes* (pp. 177-220). Chicago:  
 1055 University of Chicago Press.
- 1056 Klahr, D., & Robinson, M. (1981). Formal assessment of problem-solving and planning processes in  
 1057 preschool children. *Cognitive Psychology*, *13*(1), 113-148.
- 1058 Lai, Z. C., Moss, M. B., Killiany, R. J., Rosene, D. L., & Herndon, J. G. (1995). Executive system dysfunction  
 1059 in the aged monkey: spatial and object reversal learning. *Neurobiology of Aging*, *16*(6), 947-954.
- 1060 Limongelli, L., Boysen, S., & Visalberghi, E. (1995). Comprehension of cause-effect relations in a tool-  
 1061 using task by chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology*, *109*(1), 18-26.
- 1062 Makris, N., Papadimitriou, G. M., van der Kouwe, A., Kennedy, D. N., Hodge, S. M., Dale, A. M., . . . Tuch,  
 1063 D. S. (2007). Frontal connections and cognitive changes in normal aging rhesus monkeys: a DTI  
 1064 study. *Neurobiology of Aging*, *28*(10), 1556-1567.
- 1065 Martin-Ordas, G., Call, J., & Colmenares, F. (2008). Tubes, tables and traps: great apes solve two  
 1066 functionally equivalent trap tasks but show no evidence of transfer across tasks. *Animal*  
 1067 *Cognition*, *11*(3), 423-430.
- 1068 Menzel, E. W. (1973). Chimpanzee spatial memory organization. *Science; Science*.
- 1069 Miyake, A., Friedman, N. P., Emerson, M. J., Witzki, A. H., Howerter, A., & Wager, T. D. (2000). The unity  
 1070 and diversity of executive functions and their contributions to complex "frontal lobe" tasks: A  
 1071 latent variable analysis. *Cognitive Psychology*, *41*(1), 49-100.
- 1072 Mulcahy, N. J., & Call, J. (2006). How great apes perform on a modified trap-tube task. *Animal Cognition*,  
 1073 *9*(3), 193-199.
- 1074 Norman, D. A., & Shallice, T. (1980). Attention to action: Willed and automatic control of behavior: DTIC  
 1075 Document.
- 1076 Pan, J., Kennedy, E. H., Pickering, T., Menzel, C. R., Stone, B. W., & Fragaszy, D. (2011). Development of  
 1077 maze navigation by tufted capuchins (*Cebus apella*). *Behavioural Processes*, *86*(2), 206-  
 1078 215.
- 1079 Povinelli, D. J. (2000). *Folk physics for apes: the chimpanzee's theory of how the world works*: Oxford  
 1080 University Press, USA.
- 1081 R Development Core Team. (2011). R: A Language and Environment for Statistical Computing. Vienna,  
 1082 Austria: R Project for Statistical Computing Retrieved from <http://www.R-project.org>
- 1083 Rensch, B., & Döhl, J. (1968). Wahlen zwischen zwei überschaubaren Labyrinthwegen durch einen  
 1084 Schimpansen. *Zeitschrift für Tierpsychologie*, *25*(2), 216-231.
- 1085 Roberts, R. J., & Pennington, B. F. (1996). An interactive framework for examining prefrontal cognitive  
 1086 processes. *Developmental Neuropsychology*, *12*(1), 105-126.
- 1087 Roth, G., & Dicke, U. (2005). Evolution of the brain and intelligence. *Trends in Cognitive Sciences*, *9*(5),  
 1088 250-257.
- 1089 Salthouse, T. A., Atkinson, T. M., & Berish, D. E. (2003). Executive functioning as a potential mediator of  
 1090 age-related cognitive decline in normal adults. *Journal of Experimental Psychology: General*,  
 1091 *132*(4), 566.
- 1092 Sanz, C. M., & Morgan, D. B. (2007). Chimpanzee tool technology in the Goualougo Triangle, Republic of  
 1093 Congo. *Journal of Human Evolution*, *52*(4), 420-433.
- 1094 Scarf, D., & Colombo, M. (2009). Eye movements during list execution reveal no planning in monkeys  
 1095 (*Macaca fascicularis*). *Journal of Experimental Psychology: Animal Behavior Processes*, *35*(4),  
 1096 587.
- 1097 Scarf, D., & Colombo, M. (2010). The formation and execution of sequential plans in pigeons (*Columba livia*)  
 1098 *Behavioural Processes*, *83*(2), 179-182.
- 1099 Scarf, D., Danly, E., Morgan, G., Colombo, M., & Terrace, H. S. (2011). Sequential planning in rhesus  
 1100 monkeys (*Macaca mulatta*). *Animal Cognition*, *14*(3), 317-324.

- 1101 Seed, A. M., Call, J., Emery, N. J., & Clayton, N. S. (2009). Chimpanzees solve the trap problem when the  
1102 confound of tool-use is removed. *Journal of Experimental Psychology: Animal Behavior*  
1103 *Processes*, 35(1), 23.
- 1104 Semendeferi, K., Lu, A., Schenker, N., & Damásio, H. (2002). Humans and great apes share a large frontal  
1105 cortex. *Nature Neuroscience*, 5(3), 272-276.
- 1106 Shallice, T. (1982). Specific impairments of planning. *Philosophical Transactions of the Royal Society of*  
1107 *London. B, Biological Sciences*, 298(1089), 199-209.
- 1108 Stanford, C. B. (1996). The hunting ecology of wild chimpanzees: implications for the evolutionary  
1109 ecology of Pliocene hominids. *American Anthropologist*, 98(1), 96-113.
- 1110 Terrace, H. (1984). Simultaneous chaining: The problem it poses for traditional chaining theory.  
1111 *Quantitative analyses of behavior: Discrimination processes*, 115-138.
- 1112 van Casteren, A., Sellers, W., Thorpe, S., Coward, S., Crompton, R., Myatt, J., & Ennos, A. (2012). Nest-  
1113 building orangutans demonstrate engineering know-how to produce safe, comfortable beds.  
1114 *Proceedings of the National Academy of Sciences of the United States of America*, 109(18), 6873.
- 1115 Vlamings, P. H. J. M., Hare, B., & Call, J. (2010). Reaching around barriers: the performance of the great  
1116 apes and 3–5-year-old children. *Animal Cognition*, 13(2), 273-285.
- 1117 Vlamings, P. H. J. M., Uher, J., & Call, J. (2006). How the great apes (*Pan troglodytes*, *Pongo pygmaeus*,  
1118 *Pan paniscus*, and *Gorilla gorilla*) perform on the reversed contingency task: The effects of food  
1119 quantity and food visibility. *Journal of Experimental Psychology: Animal Behavior Processes*,  
1120 32(1), 60.
- 1121 Wellman, H. M., Fabricius, W., & Sophian, C. (1985). The early development of planning. In H. M.  
1122 Wellman (Ed.), *Children's searching: The development of search skill and spatial representation*  
1123 (pp. 123-149). Hillsdale: Erlbaum.
- 1124 Wellman, H. M., Somerville, S. C., Revelle, G. L., Haake, R. J., & Sophian, C. (1984). The development of  
1125 comprehensive search skills. *Child Development*, 472-481.
- 1126 West, R. L. (1996). An application of prefrontal cortex function theory to cognitive aging. *Psychological*  
1127 *Bulletin*, 120(2), 272.
- 1128 Willatts, P. (1989). Development of problem-solving in infancy. In A. B. Slater, G. (Ed.), *Infant*  
1129 *development* (pp. 143-182). Hillsdale: Lawrence Erlbaum Associates, Inc.
- 1130
- 1131
- 1132

1133 Table 1 Species, age, sex, rearing history, and the experiments in which the subjects participated

<b>Name</b>	<b>Species</b>	<b>Sex</b>	<b>Age</b>	<b>Rearing History</b>	<b>Experiment Participation</b>
<b>Kuno</b>	Bonobo	m	14	Nursery	1, 2
<b>Ulindi</b>	Bonobo	f	17	Mother	1
<b>Alex</b>	Chimpanzee	m	10	Nursery	1, 2
<b>Fifi</b>	Chimpanzee	f	18	Mother	1, 2
<b>Kofi</b>	Chimpanzee	f	6	Mother	1, 2
<b>Pia</b>	Chimpanzee	f	12	Mother	1, 2
<b>Riet</b>	Chimpanzee	m	33	Nursery	1
<b>Robert</b>	Chimpanzee	m	35	Nursery	1
<b>Sandra</b>	Chimpanzee	f	18	Mother	1, 2
<b>Kibara</b>	Gorilla	f	7	Mother	1
<b>Kila</b>	Orangutan	f	11	Mother	1, 2
<b>Pini</b>	Orangutan	f	23	Mother	1

1134

1135



1136 Table 2 Dependent variables and their interpretation for above-chance performance.

<b>Dependent variables</b>	<b>Interpretation</b>
Number of trials per configuration	Efficient post-error adjustment
T1 success	Sequential decision making (without planning ahead)
T1 first decision (in LoP 1 and 2)	Upcoming decisions are considered (i.e. planning)
T1 first move	Planning executed before motor response initiated

1137

1138 Table 3 Exp. 1: First trial performance as a function of the factors level of planning (LoP), change in  
 1139 direction (CiD), age of subjects, and repetition of configurations. In bold the results of the GLMM are  
 1140 presented including the estimates (Est), standard error of the mean (SEM) and P-value of each factor.  
 1141 The intercept of the GLMM represents a test of subjects' performance against the chance value. Below  
 1142 each factor the means (M), SEM and P-values of the post-hoc tests (based on the intercept of the GLMM)  
 1143 against the chance value are shown for the different levels of each factor.

Model terms	T1 Success		
	M / Est	SEM	P
<b>Intercept</b>	<b>0.71</b>	<b>0.20</b>	<b>0.001</b>
<b>LoP</b>	<b>-0.10</b>	<b>0.20</b>	<b>0.302</b>
0	0.44	0.07	<0.001
1	0.38	0.06	0.003
2	0.39	0.06	0.004
<b>CiD</b>	<b>-0.38</b>	<b>0.09</b>	<b>&lt;0.001</b>
0	0.48	0.06	0.000
1	0.33	0.06	0.092
<b>Age</b>	<b>-0.54</b>	<b>0.21</b>	<b>0.009</b>
<b>Repetition</b>	<b>0.33</b>	<b>0.09</b>	<b>&lt;0.001</b>
1	0.34	0.05	0.072
2	0.47	0.07	0.000

1144

1145

1146 Table 4: First trial (T1) performance of younger individuals (< 20 years, N=9) in Exp. 1. In bold the results  
 1147 of the GLMM are presented including the estimates (Est), standard error of the mean (SEM) and P-value  
 1148 of each factor. The intercept of the GLMM represents a test of subjects' performance against the chance  
 1149 value. Below each factor the means (M), SEM and P-values of the post-hoc tests (based on the intercept  
 1150 of the GLMM) against the chance value are shown for the different levels of each factor.

	T1 Success			T1 First decision			T1 First move		
	M / Est	SEM	p	M / Est	SEM	p	M / Est	SEM	p
<b>Intercept</b>	<b>0.99</b>	<b>0.25</b>	<b>&lt;0.001</b>	<b>0.61</b>	<b>0.15</b>	<b>&lt;0.001</b>	<b>0.54</b>	<b>0.18</b>	<b>0.003</b>
<b>LoP</b>	<b>-0.16</b>	<b>0.10</b>	<b>0.122</b>	<b>-0.13</b>	<b>0.10</b>	<b>0.207</b>	<b>-0.03</b>	<b>0.10</b>	<b>0.800</b>
0	0.53	0.06	<0.001	0.69	0.03	<0.001	0.64	0.06	0.006
1	0.44	0.07	0.001	0.63	0.06	0.009	0.63	0.07	0.003
2	0.44	0.07	0.002	0.63	0.05	0.006	0.63	0.04	0.027
<b>CiD</b>	<b>-0.43</b>	<b>0.11</b>	<b>0.000</b>	<b>-0.11</b>	<b>0.10</b>	<b>0.302</b>	<b>-0.12</b>	<b>0.10</b>	<b>0.256</b>
0	0.56	0.06	<0.001	0.67	0.04	<0.001	0.66	0.05	0.001
1	0.38	0.07	0.024	0.63	0.05	0.006	0.61	0.05	0.043
<b>Age</b>	<b>-0.11</b>	<b>0.25</b>	<b>0.663</b>	<b>-0.18</b>	<b>0.15</b>	<b>0.217</b>	<b>-0.25</b>	<b>0.17</b>	<b>0.155</b>
<b>Repetition</b>	<b>0.41</b>	<b>0.11</b>	<b>0.000</b>	<b>0.19</b>	<b>0.10</b>	<b>0.064</b>	<b>0.20</b>	<b>0.10</b>	<b>0.051</b>
1	0.38	0.06	0.028	0.61	0.03	0.052	0.59	0.04	0.069
2	0.56	0.06	<0.001	0.69	0.05	0.001	0.68	0.06	0.001

1151

1152 Table 5 Exp. 1: Number of trials per configuration of younger subjects (N=9) as a function of level of  
 1153 planning (LoP), change in direction (CiD), age of subjects, and repetition of configurations. In bold the  
 1154 results of the GLMM are presented including the estimates (Est), standard error of the mean (SEM) and  
 1155 P-value of each factor. The intercept of the GLMM represents a test of subjects' performance against the  
 1156 chance value. Below each factor the means (M), SEM and P-values of the post-hoc tests (based on the  
 1157 intercept of the GLMM) against the chance value are shown for the different levels of each factor.

Model terms	Number trials		
	M / Est	SEM	P
<b>Intercept</b>	-0.20	0.17	0.246
<b>LoP</b>	<b>0.06</b>	<b>0.05</b>	<b>0.185</b>
0	2.83	0.39	0.032
1	3.72	0.48	0.754
2	3.29	0.60	0.198
<b>CiD</b>	<b>0.07</b>	<b>0.08</b>	<b>0.440</b>
0	3.11	0.53	0.274
1	3.45	0.52	0.307
<b>Age</b>	<b>-0.12</b>	<b>0.12</b>	<b>0.298</b>
<b>Repetition</b>	<b>-0.25</b>	<b>0.03</b>	<b>&lt;0.001</b>
1	4.10	0.57	0.882
2	2.46	0.53	0.002

1158

1159 Table 6 Exp. 2: First trial performance as a function of level of planning (LoP), change in direction (CiD),  
 1160 age of subjects, and repetition of configurations. In bold the results of the GLMM are presented including  
 1161 the estimates (Est), standard error of the mean (SEM) and P-value of each factor. The intercept of the  
 1162 GLMM represents a test of subjects' performance against the chance value. Below each factor the means  
 1163 (M), SEM and P-values of the post-hoc tests (based on the intercept of the GLMM) against the chance  
 1164 value are shown for the different levels of each factor.

Model terms	T1 Success			T1 First decision		
	M / Est	SEM	P	M / Est	SEM	P
<b>Intercept</b>	<b>1.92</b>	<b>0.13</b>	<b>&lt;0.001</b>	<b>0.31</b>	<b>0.11</b>	<b>0.006</b>
<b>LoP</b>	<b>-0.27</b>	<b>0.12</b>	<b>0.018</b>	<b>-0.22</b>	<b>0.11</b>	<b>0.054</b>
0	0.55	0.09	<0.001	0.63	0.08	0.003
1	0.53	0.05	<0.001	0.61	0.04	0.000
2	0.40	0.05	<0.001	0.50	0.04	1.000
<b>CiD</b>	<b>-0.42</b>	<b>0.12</b>	<b>&lt;0.001</b>	<b>-0.31</b>	<b>0.11</b>	<b>0.008</b>
0	0.71	0.05	<0.001	0.74	0.05	0.000
1	0.41	0.05	<0.001	0.52	0.04	0.589
2	0.44	0.07	<0.001	0.54	0.05	0.419
<b>Age</b>	<b>-0.40</b>	<b>0.13</b>	<b>0.002</b>	<b>-0.28</b>	<b>0.11</b>	<b>0.016</b>
<b>Repetition</b>	<b>0.13</b>	<b>0.11</b>	<b>0.252</b>	<b>0.00</b>	<b>0.11</b>	<b>1.000</b>
1	0.46	0.05	<0.001	0.58	0.04	0.049
2	0.52	0.06	<0.001	0.58	0.04	0.041

1165

1166

1167 Table 7 : Output of GLMM (Est estimates, SEM standard error of the mean, and P-value of each factor.)  
 1168 comparing the T1 first decision performance across Experiment 1 and 2 (Number of traps), level of  
 1169 planning (LoP), age of subjects, and repetition of configurations.

Model terms	T1 First decision		
	Est	SEM	P
<b>Intercept</b>	0.53	0.10	<0.001
<b>Number of traps</b>	-0.23	0.08	0.004
<b>LoP</b>	-0.17	0.09	0.043
<b>Age</b>	-0.30	0.10	0.002
<b>Repetition</b>	0.14	0.08	0.086

1170

1171 Table 8 Exp. 2: Number of trials per configuration as a function of level of planning (LoP), change in  
 1172 direction (CiD), age of subjects, and repetition of configurations. In bold the results of the GLMM are  
 1173 presented including the estimates (Est), standard error of the mean (SEM) and P-value of each factor.  
 1174 The intercept of the GLMM represents a test of subjects' performance against the chance value. Below  
 1175 each factor the means (M), SEM and p-values of post-hoc tests (based on the intercept of the GLMM)  
 1176 against the chance value are shown for the different levels of each factor.

Model terms	Number of trials		
	M / Est	SEM	P
<b>Intercept</b>	<b>-1.36</b>	<b>0.06</b>	<b>&lt;0.001</b>
<b>LoP</b>	<b>0.14</b>	<b>0.05</b>	<b>&lt;0.001</b>
0	2.04	0.29	<0.001
1	2.21	0.27	<0.001
2	2.90	0.24	<0.001
<b>CiD</b>	<b>0.18</b>	<b>0.05</b>	<b>0.001</b>
0	1.45	0.12	<0.001
1	2.76	0.32	<0.001
2	2.56	0.22	<0.001
<b>Age</b>	<b>0.21</b>	<b>0.05</b>	<b>&lt;0.001</b>
<b>Repetition</b>	<b>-0.14</b>	<b>0.04</b>	<b>&lt;0.001</b>
1	2.72	0.31	<0.001
2	2.05	0.23	<0.001

1177

1178 Table 9 Exp. 3: First trial performance as a function of level of planning (LoP), change in direction (CiD),  
 1179 age of subjects, and repetition of configurations. In bold the results of the GLMM are presented including  
 1180 the estimates (Est), standard error of the mean (SEM) and P-value of each factor. The intercept of the  
 1181 GLMM represents a test of subjects' performance against the chance value. Below each factor the means  
 1182 (M), SEM and p-values of the post-hoc tests (based on the intercept of the GLMM) against the chance  
 1183 value are shown for the different levels of each factor.

1184

Model terms	T1 Success			T1 First decision		
	M / Est	SEM	P	M / Est	SEM	P
<b>Intercept</b>	<b>1.85</b>	<b>0.52</b>	<b>&lt;0.001</b>	<b>0.97</b>	<b>0.31</b>	<b>0.001</b>
<b>LoP</b>	<b>-0.69</b>	<b>0.11</b>	<b>&lt;0.001</b>	<b>-0.72</b>	<b>0.11</b>	<b>&lt;0.001</b>
0	0.84	0.03	<0.001	0.88	0.02	<0.001
1	0.67	0.03	0.007	0.73	0.03	0.001
2	0.54	0.03	<0.001	0.58	0.03	0.110
<b>CiD</b>	<b>-0.07</b>	<b>0.11</b>	<b>0.494</b>	<b>-0.06</b>	<b>0.11</b>	<b>0.597</b>
0	0.69	0.03	0.003	0.73	0.02	<0.001
1	0.67	0.03	<0.001	0.72	0.03	0.008
<b>Age</b>	<b>0.34</b>	<b>0.13</b>	<b>0.007</b>	<b>0.26</b>	<b>0.12</b>	<b>0.025</b>
4 y	0.62	0.03	<0.001	0.68	0.03	<0.001
5 y	0.74	0.03	<0.001	0.77	0.03	<0.001
<b>Repetition</b>	<b>0.50</b>	<b>0.07</b>	<b>&lt;0.001</b>	<b>0.35</b>	<b>0.07</b>	<b>&lt;0.001</b>
1	0.59	0.03	<0.001	0.67	0.02	0.001
2	0.77	0.03	<0.001	0.78	0.03	<0.001

1185



1186 Table 10 Exp 3: T1 first decision performance of 4- and 5-year-old children is presented. M mean, SEM  
 1187 standard error of the mean, P-value of post-hoc tests (based on the intercept of the GLMM) against the  
 1188 chance value.

		4-year-olds			5-year-olds		
		M	SEM	P	M	SEM	P
<b>LoP</b>	0	0.84	0.03	<0.001	0.91	0.03	<0.001
	1	0.65	0.04	0.001	0.80	0.04	<0.001
	2	0.55	0.04	0.267	0.60	0.04	0.187
<b>CiD</b>	0	0.69	0.03	<0.001	0.78	0.03	<0.001
	1	0.68	0.04	<0.001	0.76	0.03	0.004

1189

1190 Table 11 Exp. 3: Number of trials per configuration as a function of level of planning (LoP), change in  
 1191 direction (CiD), age of subjects, and repetition of configurations. In bold the results of the GLMM are  
 1192 presented including the estimates (Est), standard error of the mean (SEM) and P-value of each factor.  
 1193 The intercept of the GLMM represents a test of subjects' performance against the chance value. Below  
 1194 each factor the means (M), SEM and p-values of the post-hoc tests (based on the intercept of the GLMM)  
 1195 against the chance value are shown for the different levels of each factor.

1196

Model terms	Number of trials		
	M / Est	SEM	P
<b>Intercept</b>	<b>-0.94</b>	<b>0.05</b>	<b>&lt;0.001</b>
<b>LoP</b>	<b>0.10</b>	<b>0.03</b>	<b>0.001</b>
0	1.38	0.09	<0.001
1	1.54	0.08	<0.001
2	1.75	0.08	<0.001
<b>CiD</b>	<b>0.03</b>	<b>0.03</b>	<b>0.320</b>
0	1.51	0.07	<0.001
1	1.60	0.09	<0.001
<b>Age</b>	<b>-0.08</b>	<b>0.04</b>	<b>0.042</b>
4 y	1.68	0.10	<0.001
5 y	1.44	0.08	<0.001
<b>Repetition</b>	<b>-0.18</b>	<b>0.02</b>	<b>&lt;0.001</b>
1	1.84	0.11	<0.001
2	1.28	0.04	<0.001

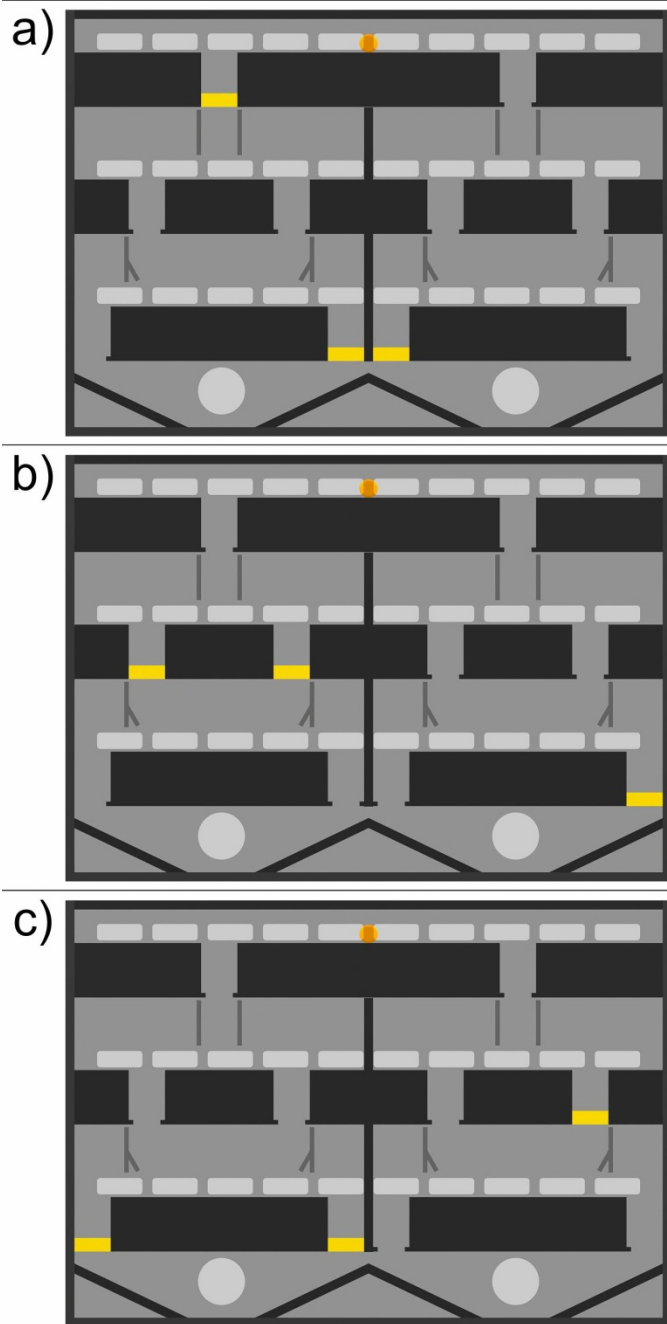
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1198

1199 Fig.1 Illustration of an ape working on the maze apparatus. The reward is shown in the starting  
1200 position on the uppermost level. The subjects could move the reward via the slits in the front  
1201 side of the apparatus. The shown trap configuration is an example of level of planning (LoP) 1  
1202 and changes in direction (CiD) 1. The openings in the backside of the apparatus that allowed  
1203 baiting and entering/removing the yellow trap elements are not depicted here for the sake of  
1204 convenience.

1205



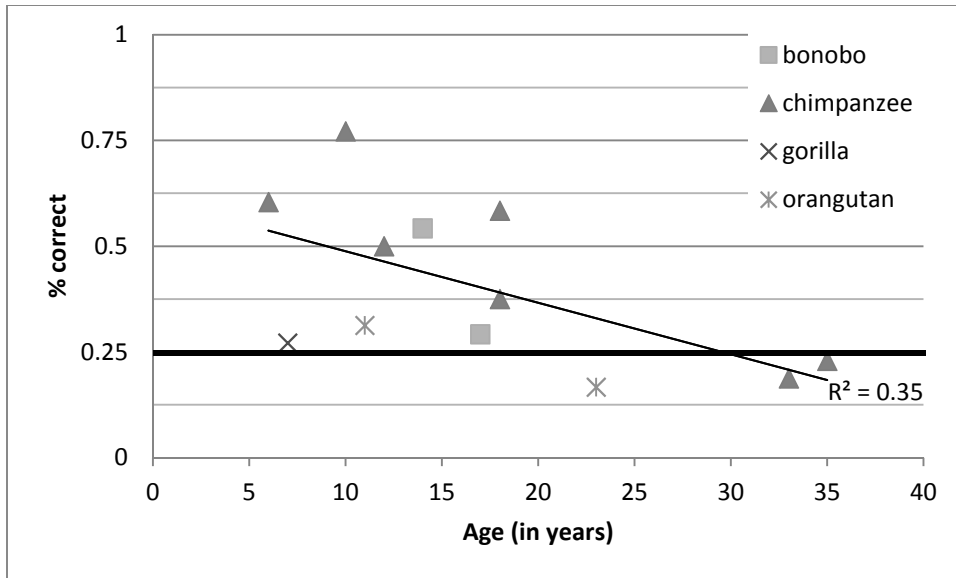
1206

1207 Fig. 2 Examples of different trap configurations employed in the current study according to their

1208 level of planning (LoP) and changes in direction (CiD). a LoP 0, CiD 0; b LoP 1, CiD 1; c LoP 2,

1209 CiD 1

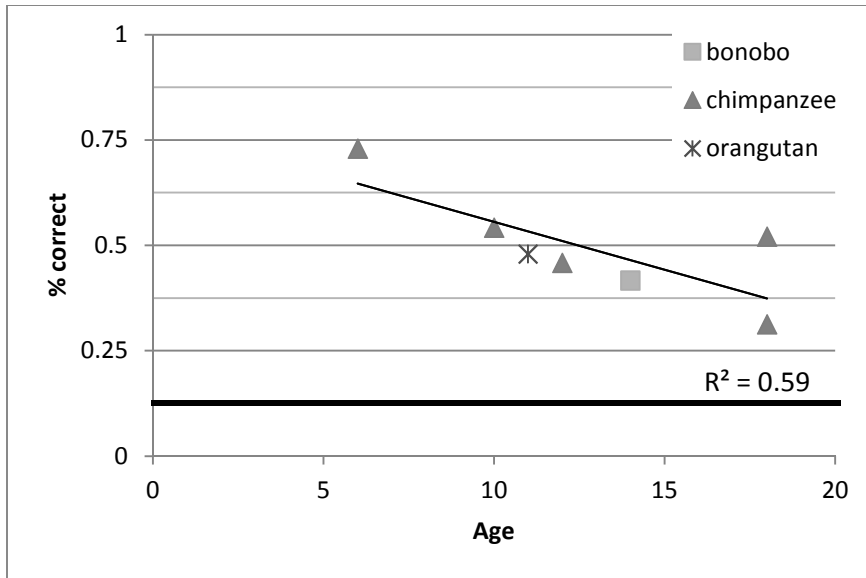
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1212 Fig.3 Exp. 1: Trial 1 success as a function of age and species

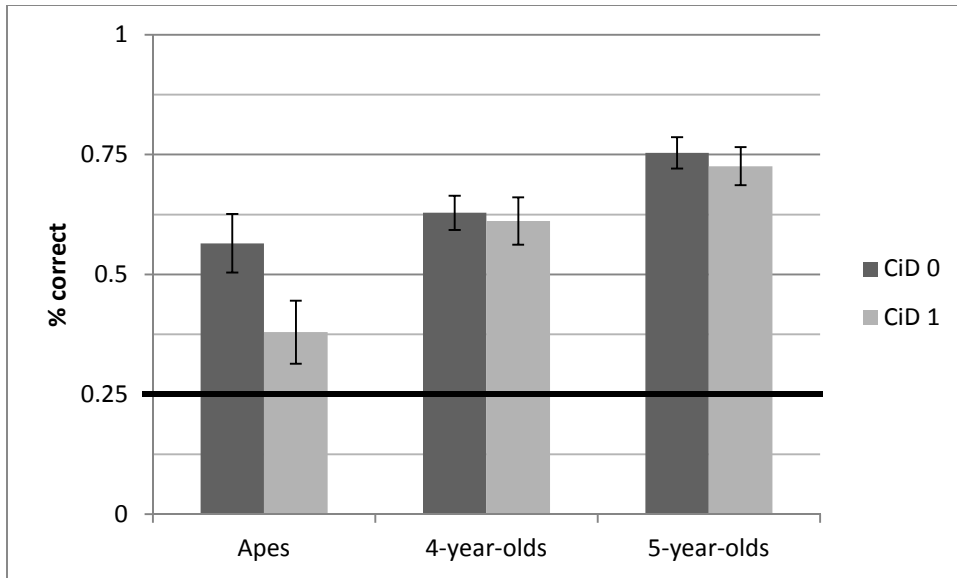
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1214

1215 Fig.4 Exp. 2: Trial 1 success as a function of age and species

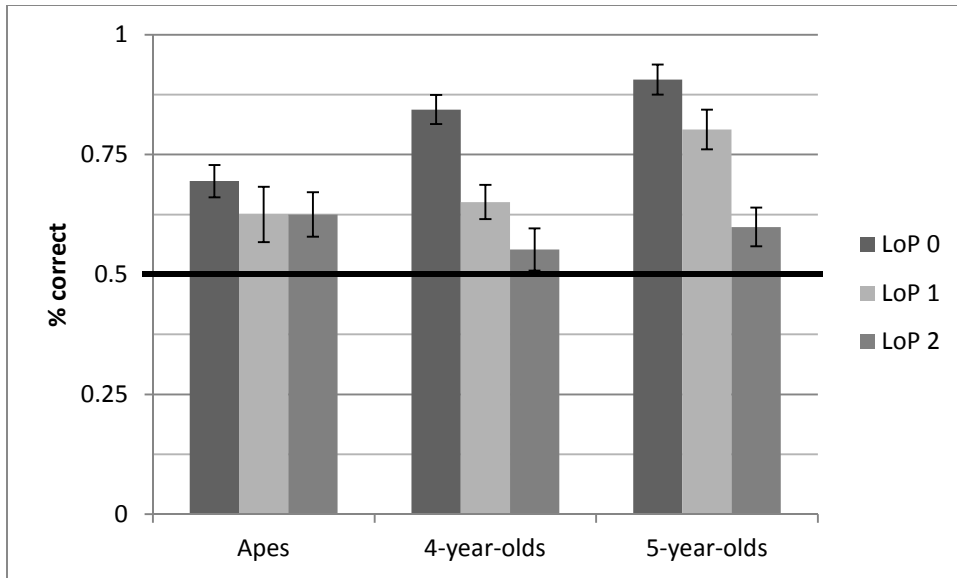
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1218 Fig.5 Trial 1 success as a function of subject groups (younger nonhuman apes, 4-year-old  
1219 children, and 5-year-old children) and changes in direction (CiD)

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1222 Fig.6 First decision in Trial 1 as a function of subject groups (younger nonhuman apes, 4-year-  
1223 old children, and 5-year-old children) and level of planning (LoP)

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