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3 **Optional-Switch Cognitive Flexibility in Primates: Chimpanzees' (*Pan troglodytes*)**

4 **Intermediate Susceptibility to Cognitive Set**

5

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**Abstract**

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Within human problem solving, the propensity to use a familiar approach, rather than switch to a more efficient alternative is pervasive. This susceptibility to ‘cognitive set’ prevents optimization by biasing response patterns toward known solutions. In a recent study, which utilized nonverbal touch screen task, baboons exhibited a striking ability to deviate from their learned strategy to utilize a more efficient shortcut. Humans, on the other hand, displayed the opposite response pattern and almost exclusively used a less efficient, but familiar, response. In the current study, we sought to further explore variation in susceptibility to cognitive set within the primate lineage by conducting the LS-DS task with ten chimpanzees (*Pan troglodytes*). Using multilevel multinomial modeling, we found that chimpanzees’ shortcut-use was intermediate to baboons’ and humans’. However, unlike either baboons or humans, there was pronounced inter- and intra-individual variability in chimpanzees’ shortcut-use. Additionally, a subset of chimpanzees employed a unique solution, wherein they switched strategies mid-trial. Further, we found that chimpanzees did not exhibit switch costs when switching between the learned strategy and the shortcut, but humans did. We propose that differences in abstract rule encoding may underlie differences in susceptibility to cognitive set on the LS-DS task within the primate lineage.

Keywords: Cognitive Flexibility, Evolution, Cognitive Set, Optional-Switch, Primates

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## Introduction

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Adaptive behavior is predicated upon flexible strategy-use, yet such plasticity is complex. Flexible responses must integrate external environmental cues with internal inputs, such as past experience. Furthermore, when a past strategy is no longer the most appropriate, flexible behavior requires extinguishing that previous response and switching to a more efficient strategy. Here, we define cognitive flexibility as the ability to incorporate both known solutions and innovated or acquired novel solutions in a contextually appropriate manner (Buttelmann & Karbach, 2017; Lehner, Burkart, & Schaik, 2011).

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Our current understanding of how cognitive flexibility may have evolved is limited. Cognitive flexibility is a multifaced construct, comprised of one's abilities to innovate, switch between, and adopt strategies; yet, it is often only studied in a single context. Typical forced-switch metrics, like reversal or card sorting tasks, *require* subjects to switch strategies. Subjects learn a solution that, at some later point, either a) stops working, or or b) they are instructed not to use anymore. Using forced-switch tasks, the role of cognitive flexibility in developmental and pathological variation in executive functioning has been studied extensively (Doebel & Zelazo, 2015; Luwel, Schillemans, Onghena, & Verschaffel, 2009; Rhodes, 2004; Sullivan et al., 1993; Zelazo et al., 2003). However, within the primate lineage, forced-switch measures yield somewhat conflicting results.

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In reversal tasks, wherein a previously successful strategy stops working, humans (even 3-5 year old children) are less perseverative than apes, which in turn are less perseverative than monkeys (Harlow, 1949; Rumbaugh, Savage-Rumbaugh, &

71 Washburn, 1996). That said, with practice (~100 problems), even monkeys are able to  
72 perform at or near ceiling, suggesting that their initial perseveration is due to slower  
73 acquisition of the new rule rather than difficulty shifting between strategies (Harlow,  
74 1949).

75 Card sorting tasks have been used extensively to measure switching ability across  
76 primate (and other mammal) species (Brown & Tait, 2016). There are many versions of  
77 this paradigm (e.g., Wisconsin Card Sorting Task, Dimensional Change Card Sort and  
78 Conceptual Set Shifting Task); however, each requires subjects to sort a series of  
79 multivalent cards, first according to one dimension (e.g., color) and then another (e.g.  
80 shape; Berg, 1948; Zelazo et al., 2003). Adult humans master the first rule within a few  
81 trials, while other non-human primate species take much longer on similar tasks  
82 (baboons:  $M = 178$ ; macaques:  $M = 137$ ; chimpanzees:  $M = \sim 300-600$  marmosets:  $M \sim$   
83 180); however, both human and non-human primates exhibit similar degrees of  
84 perseveration following the first rule switch (Bonté, Flemming, & Fagot, 2011; Lacreuse,  
85 Parr, Chennareddi, & Herndon, 2018; Moore, Killiany, Herndon, Rosene, & Moss, 2005;  
86 Roberts, Robbins, & Everitt, 1988).

87 Moreover, in some ways monkeys have been found to be more efficient than  
88 humans at switching between known strategies. Switch costs, or deficits in response time  
89 or accuracy, occur when switching from one familiar strategy to another (Brass, Derrfuss,  
90 & von Cramon, 2007). They are thought to arise from the shift in neural activity  
91 associated with how each strategy guides behavior (Lemaire, Luwel, & Brun, 2017;  
92 Luwel et al., 2009; Meiran, 1996). Both human children and adults exhibit switch costs  
93 on trials which require them to switch from one familiar strategy to another (Arrington &

94 Logan, 2004; Ionescu, 2012; Rogers & Monsell, 1995; Zelazo, 2008), even after  
95 extensive practice (Stoet & Snyder, 2007). Yet, rhesus macaques (*Macaca mulatta*)  
96 seemingly do not (Stoet & Snyder, 2003; however see: Caselli & Chelazzi, 2011; Huguet,  
97 Barbet, Belletier, Monteil, & Fagot, 2014). However, how switch costs affect other non-  
98 human primate species remains unclear.

99         The current understanding of strategy-switching is dominated by forced-switch  
100 tasks. However, the ability of forced-switch metrics to capture the breadth of cognitive  
101 flexibility is up for debate (Arrington & Logan, 2004; Deak & Wiseheart, 2015; Ionescu,  
102 2012, 2017). Forced strategy switches are certainly not the only contexts in which an  
103 animal might require cognitive flexibility. Often, multiple solutions are present within a  
104 problem space and must be selected between for optimal behavior (Brosnan & Hopper,  
105 2014). *Optional-switch* paradigms account for some of this complexity by allowing for  
106 multiple ‘correct’ solutions that differ in overall efficiency (e.g., time spent, reward  
107 value, reduced risk of predation, etc.).

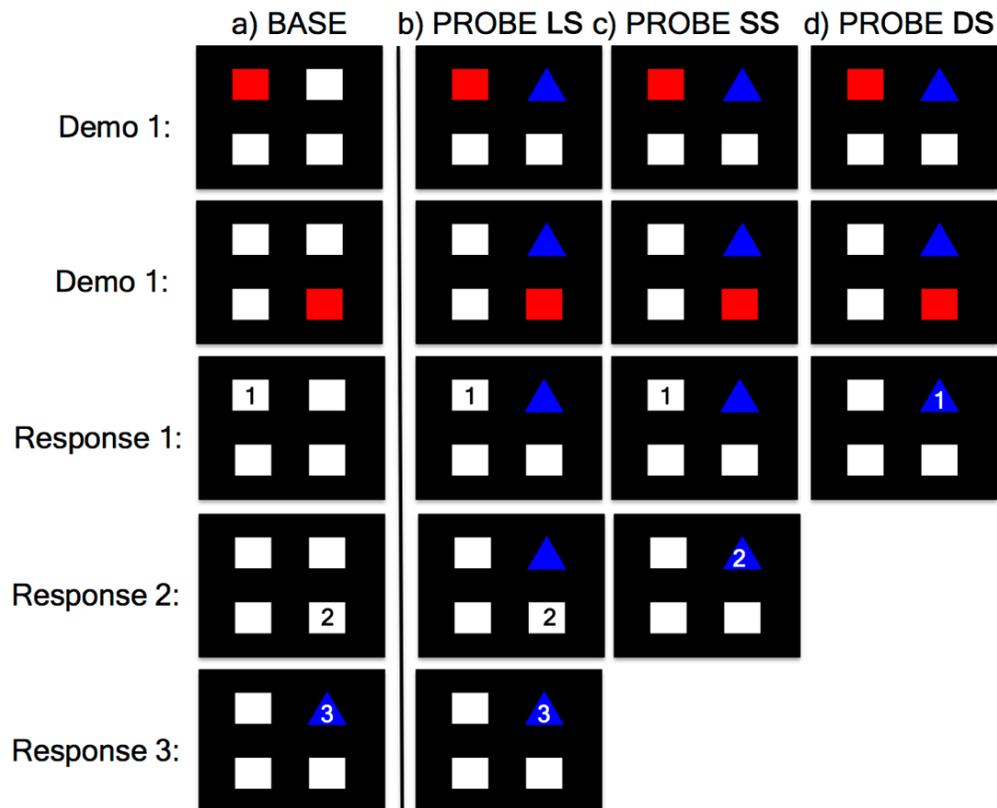
108         Interestingly, humans often fail to select the most appropriate response on  
109 optional-switch tasks, primarily when adopting a better alternative would require them to  
110 deviate from a learned or familiar method (Adamson, 1952; Aftanas & Koppenaal, 1962;  
111 Bilalić, Mcleod, & Gobet, 2008; Chrysikou & Weisberg, 2005; Crooks & McNeil, 2009;  
112 Duncker & Lees, 1945; Luchins, 1942; Luchins & Luchins, 1950; Ruscio & Amabile,  
113 1999; Sweller, Mawer, & Howe, 1982). We will refer to this ability of learned solutions  
114 to block better alternatives, as cognitive set. In a previous study, Pope, Meguerditchian,  
115 Hopkins, & Fagot (2015) compared baboons’ and humans’ susceptibility to cognitive set  
116 using a nonverbal ‘Learned Strategy-Direct Strategy’ (LS-DS) touch screen task. In this

117 task, subjects become familiar with a three-step (Square1 → Square2 → Triangle) learned  
118 strategy (LS; see Figure 1a and Video S1) and are then presented with experimental trials  
119 in which they can either use the LS (See Figure 1b) *or* a more direct strategy (DS or the  
120 shortcut) by skipping the Square1 → Square2 sequence and going straight for the Triangle  
121 (See Figure 1d and Video S2). The study found that, remarkably, all 15 baboon subjects  
122 immediately switched to the DS when it became available, using it in 99% of trials. By  
123 comparison, only 6.7% of humans used the DS in more than 50% of trials, demonstrating  
124 that humans but not baboons were highly susceptible to cognitive set on the LS-DS task.

125         In the current study, we explored how non-human apes fit into this dialogue.  
126 Indeed, many social learning studies have investigated non-human apes' abilities to  
127 retrieve food from an apparatus by switching away from a familiar strategy, after  
128 watching a demonstration of a more efficient alternative. A large number of these studies  
129 find that non-human apes struggle to switch to the demonstrated strategy (Davis, 2017;  
130 Davis, Vale, Schapiro, Lambeth, & Whiten, 2016; Gruber, Muller, Reynolds, Wrangham,  
131 & Zuberbuhler, 2011; Hrubesch, Preuschoft, & van Schaik, 2009; Manrique & Call,  
132 2015; Marshall-Pescini & Whiten, 2008; Price, Lambeth, Schapiro, & Whiten, 2009).  
133 However, within the context of social learning, it is difficult to parse out perseverative  
134 behaviors that arise from an inability to learn from a demonstration, from those that are  
135 products of cognitive inflexibility. In fact, other studies report compelling evidence for  
136 flexible strategy-use in apes, especially when the alternative solution requires relatively  
137 simple modifications or reaps a better reward (Davis, Schapiro, Lambeth, Wood, &  
138 Whiten, 2018; Harrison & Whiten, 2018; Jacobson & Hopper, 2019; Lehner et al., 2011;  
139 Manrique, Völter, & Call, 2013; Van Leeuwen, Cronin, Schutte, Call, & Haun, 2013;

140 Yamamoto, Humle, & Tanaka, 2013). Thus, the extent to which non-human apes are  
 141 capable of flexible strategy-use within an optional-switch context is also unclear.

142 The current study had two aims. First, we wanted to explore chimpanzees'  
 143 susceptibility to cognitive set on the LS-DS task. Importantly, in the LS-DS task, the  
 144 shortcut is a familiar component of the learned sequence; therefore, using it does not  
 145 require learning new affordances or watching a demonstration. Second, we sought to  
 146 contextualize these findings by comparing chimpanzees' response patterns on the LS-DS  
 147 task to those of baboons and humans, previously reported in (Pope et al., 2015).



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149 **Figure 1.** The LS-DS Task. a) BASE and b-d) PROBE trials depicting the Top left →  
 150 Bottom right → Top right configuration. On PROBE trials, subjects may utilize any of  
 151 three response strategies to be correct: b) the learned strategy (LS), c) the switch strategy

152 (SS), or d) the direct strategy (DS). Numbers indicate the correct Response 1, Response  
153 2, and Response 3 for this configuration. Also see Video S1.

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## Methods

### 156 Chimpanzee Methods

157 **Subjects and General Procedure.** We tested 10 captive-born chimpanzee  
158 subjects, five females ( $M \pm SD = 30.9 \pm 8.0$  years, range: 21-40 years) and five males  
159 ( $M \pm SD = 25.4 \pm 2.7$  years, range: 23-30 years) located at the Yerkes National Primate  
160 Research Center in Atlanta, Georgia, USA. The LS-DS was programmed using EPrime  
161 (version 2.0, Psychology Software Tools, Pittsburgh, PA, USA) and administered using a  
162 19-inch touch monitor (1939L Open-Frame Touchmonitor, Elo Touch Solutions,  
163 Milpitas, CA, USA) affixed to a metal housing, which was temporarily attached to  
164 subjects' home enclosure during testing. Each testing session lasted roughly 20 minutes.  
165 Subjects' correct responses were rewarded with juice or small pieces of fruit or  
166 vegetables, depending on their preferences or dietary restrictions. All testing was  
167 approved by the Emory University IACUC.

168 **LS-DS Training Phase.** Chimpanzees completed four LS-DS training levels  
169 (Table 1 & Video S2). During LS-DS training, subjects are presented with a  
170 demonstration phase wherein two squares (Square1 and Square2) flash red in sequence,  
171 and a response phase wherein they select the locations of Square1 and Square2 in the  
172 demonstrated order. For each trial, the locations of Square1 and Square2 are randomly  
173 assigned to a screen quadrant (e.g. top left, top right, bottom left, bottom right). In the  
174 final training level, subjects first select Square1 and Square 2, then a triangle which

175 appears in one of the remaining quadrants. Incorrect responses resulted in a 3 second  
 176 green delay screen. Accuracy was assessed after each block of 24 trials. To progress to  
 177 the next training level, subjects were required to achieve >80% accuracy, twice. As levels  
 178 progress, the time each square is demonstrated decreases and the number of response  
 179 options increases (up to four). Note that Training 1.5 was a deviation from previous LS-  
 180 DS training methods and consisted of trials identical to Training 1 (Training1.5a)  
 181 randomly interspersed with trials in which four squares were shown but only one flashed  
 182 red (Training1.5b). By the end of training, subjects were proficient in using the three step  
 183 Square1→Square2→Triangle sequence (i.e. the learned strategy or **LS**).  
 184

**Table 1.** *Learned Strategy–Direct Strategy Training Levels*

Level	Demonstration	Response	Required Responses
	Speed	Options	
Training 1	250ms/square	2 Squares	Square 1 + Square 2
Training 1.5a	250ms/square	2 Squares	Square 1 + Square 2
Training 1.5b	250ms/square	4 Squares	Square 1
Training 2	250ms/square	4 Squares	Square 1 + Square 2
Training 3	150ms/square	4 Squares	Square 1 + Square 2 + Triangle

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186 We encountered several difficulties during training that required procedural  
 187 adjustments. First, at the beginning of Training 3, five of the ten chimpanzee subjects  
 188 would not select the triangle. In order to avoid their giving up on the task altogether, after  
 189 several unsuccessful sessions we opted to briefly modify the program (see Video S2).

190 Thus, for five of the ten subjects, after they had correctly selected Square1 → Square2,  
191 the triangle appeared in one of the two remaining places (like normal) but the other  
192 response options disappeared, such that all that was left on the screen was the triangle.  
193 Once subjects consistently touched the triangle (# of modified trials per subject = 36, 18,  
194 41, 153, 21), they were switched back to the regular version of Training3 for all  
195 remaining trials. Second, training duration varied from several months to more than a  
196 year, depending on the subject, and at some points motivation appeared to dwindle  
197 substantially. If this occurred, we enhanced their food reward or instated a 5 second (as  
198 opposed to the normal 3 second) delay following incorrect responses. Third, for Training  
199 3, even if subjects were excluding their previous selections, the likelihood of being  
200 correct in any given trial simply by chance is 4.17% (Response 1 = 1/4, Response 2 =  
201 1/3, and Response 3 = 1/2). Therefore, evidenced by considerably higher than chance  
202 accuracy scores (in one case a subject had achieved above 75% accuracy nine times)  
203 many subjects grasped the LS, yet failed to reach the >80% criterion twice. After several  
204 months, we opted to adjust the Training 3 accuracy requirements such that a subject  
205 needed to achieve either greater than 80% twice, greater than 75% three times, or greater  
206 than 70% five times in order to progress to the experimental trials.

207 **LS-DS Experimental Phase.** Immediately after training, subjects completed 96  
208 experimental trials, comprised of 48 PROBE and 48 BASE condition trials. In the  
209 PROBE condition, the Triangle appears alongside the Square1→Square2 demonstration  
210 and remains visible on the response screen (see Fig. 1b-d). Thus, in PROBE trials,  
211 subjects can then either continue to use their learned strategy,  
212 Square1→Square2→Triangle (the LS) or they can simply ignore the demonstration and

213 select the Triangle (i.e. the DS or shortcut). Additionally, the task permits a third strategy  
214 wherein subjects seemingly initiate the LS by selecting the first square but then switch to  
215 the DS by skipping the second square and instead selecting the triangle  
216 (Square1 → Triangle; Figure 1c). This ‘switch strategy’ (SS) was not reported in previous  
217 studies, as it occurred so rarely (Pope et al., 2015). In the BASE (baseline) condition,  
218 trials appear identical to Training 3 trials. However, if the subjects select the triangle’s  
219 hidden location, they are scored and rewarded as if they had used the DS or the SS. This  
220 was done to ensure that trends in shortcut use could not be attributed to accident.

221 In summary, subjects were extensively trained to reproduce the two-square  
222 demonstration and then touch the triangle but when the triangle was already present  
223 (PROBE trials) they could forego this learned strategy and directly select the triangle for  
224 a more immediate reward.

225

## 226 **Comparative Methods**

227 A primary aim of this study was to compare the chimpanzees’ responses on the  
228 LS-DS task to those of baboons and humans, which were previously collected and  
229 reported in Pope et al. (2015).

230 **Subjects and General Procedure.** Baboon data were collected from 15 socially  
231 housed baboons, nine females ( $M \pm SD = 5.1 \pm 2.3$  years, range: 1.8-9.1 years) and six  
232 males ( $M \pm SD = 5.3 \pm 2.5$  years, range: 2.3-9.3 years) located at the CNRS Station de  
233 Primatologie in Rousset-sur-Arc, France. The task was administered via ten automated  
234 learning devices for monkeys (ALDMs; Fagot & Paleressompouille, 2009) and was  
235 approved by the local Provence Alpes Cote d’Azur ethics committee for experimental

236 animal research. Human data were collected from 104 humans; 63 females ( $M \pm SD =$   
237  $27.9 \pm 17.6$  years, range: 7-68 years), 40 males ( $M \pm SD = 29.2 \pm 17.2$ , range: 7-68 years)  
238 and 1 participant who preferred to identify as neither male nor female (17 years) at a  
239 temporary testing booth set up at Zoo Atlanta in Atlanta, Georgia, USA. Human testing  
240 was approved by the Zoo Atlanta Research Committee and the Georgia State University  
241 Institutional Review Board.

242 **LS-DS Training and Experimental Phases.** As reported in Pope et al. (2015),  
243 baboons and humans completed Training levels 1, 2, and 3 (Table 1). The experimental  
244 phase consisted of 720 trials for baboons (576 BASE and 144 PROBE, this is a 4:1 ratio),  
245 96 trials for humans 11 years and older (48 BASE and 48 PROBE) and 48 trials for  
246 humans under 11 (24 BASE and 24 PROBE).<sup>1</sup> As in the original analysis, we included  
247 only the first 48 BASE and 48 PROBE trials for the baboon data in order to compare  
248 initial strategy-use across species; however baboon strategy-use remained consistent  
249 throughout the entire experimental phase.

250

## 251 **Analyses**

### 252 **General**

253 To measure differences between continuous variables such as response time or  
254 number of trials, we used linear mixed-effects models. To measure differences in  
255 accuracy error patterns, we used logistic mixed-effects models with a binomial error  
256 structure. Subject ID was included as a random effect in all models. We used the *lme4*

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<sup>1</sup> As before, we argue that the 4:1 ratio of BASE to PROBE trials that was received by baboons would only serve to enhance LS-use.

257 package (Bates, Mächler, Bolker, & Walker, 2015) in R 3.5.2 (R Core Team, 2019) to fit  
258 the models, likelihood ratio tests using single-term deletions to assess the test predictors'  
259 importance, and the *emmeans* package (Lenth, 2018) to compute pairwise contrasts, with  
260 the Tukey multiple comparison correction.

261

## 262 **Training Phase**

263 **Training and Species.** To analyze differences in the number of training trials  
264 between species, we calculated the number of trials each subject completed. Species and  
265 training level (1, 2, or 3) were included as fixed effects.<sup>2</sup>

266 **Training Errors.** To analyze differences in accuracy between each step (Step 1:  
267 Square 1, Step 2: Square 2, and Step 3: Triangle) of the response in Training 3, we  
268 calculated conditional accuracies for each step. For example, if the participant correctly  
269 selected Square 1, we calculated the proportion of trials in which they then correctly  
270 selected Square 2. Species and step (Square 1, Square 2, or Triangle) were included as  
271 fixed effects.

272 To analyze baboons' and chimpanzees' Training 2 errors, we isolated incorrect  
273 Response 1 trials that were preceded by a correct trial. For each incorrect Response 1, we  
274 determined whether the erroneous selection was a repetition of either Response 1 or  
275 Response 2 of the preceding trial. For example, if the correct response to the preceding  
276 trial was Bottom Left → Top Left and the erroneous selection was Bottom Left, this was  
277 classified as a previous Response 1 error (Previous1); similarly, if the erroneous selection

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<sup>2</sup> Chimpanzees' Training 1.5 trials were grouped with their Training 1 trials; however, the results were unchanged when they were combined with Training 2 or excluded.

278 was Top Left, this was classified as a previous Response 2 error (Previous2). We also  
279 identified trials in which subjects selected the Square2 location first. For example, if the  
280 demonstration depicted Bottom Left → Bottom Right and the erroneous Response 1 was  
281 Bottom Right this would be classified as a reversal error (Reversal). If driven by chance,  
282 we would expect errors to fall within these error types 33.3% of the time (one out of the  
283 three erroneous response options). We compared the rates of Previous1, Previous2, and  
284 Reversal error types for each species to chance ( $\mu = .33$ ) using one-way t-tests.

285

## 286 **Experimental Phase**

287 **Strategy-Use Models.** For each trial, subjects' responses could fall into one of  
288 four categories: incorrect, LS, SS, or DS. Thus, for each subject, the proportion of trials  
289 in which each strategy was used is constrained by the proportion of trials in which each  
290 other strategy was used. To best understand how strategy-use differed between subjects  
291 and across species, we decided to use Bayesian multilevel multinomial modeling. This  
292 allowed us to assess the probability of observing LS, SS, DS responses (excluding  
293 incorrect trials) within the same model.<sup>3</sup> We fit three models to these data. Each model  
294 was fit using Hamiltonian Monte Carlo estimations, using the *Rstan* and *brms* packages  
295 (Bürkner, 2017; Stan Development Team, 2018). For all models, we ran 3 chains of 4000  
296 iterations to optimize model convergence, judged by the R-hat Gelman and Rubin  
297 convergence diagnostic (McElreath, 2015).

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<sup>3</sup> We report frequentist statistics similar to our previous analyses (Pope, Fagot, Meguerditchian, Washburn, & Hopkins, 2018; Pope et al., 2015) alongside Figure S3.

298 Model 0 included only the random effect of subject ID. In addition to the random  
299 effect of subject ID, Model 1 included the main effects of species (Baboon, Chimpanzee,  
300 or Human), condition (BASE or PROBE), sex (Female<sup>4</sup> or Male), age (continuous), and  
301 training experience (continuous). To account for the substantial species difference in ages  
302 sampled, age values were centered around the age of sexual maturity averaged across  
303 males and females, for each species: baboons = 4.5, chimpanzees = 8.6, humans = 13.5  
304 years (Figure S1; De Magalhaes & Costa, 2009). To account for the large species  
305 differences in total number of training trials, this variable was z-transformed. Finally,  
306 Model 2 included the random and fixed effects from Model 1, and the interaction of  
307 species\*condition. Models were compared using the Widely Applicable Information  
308 Criteria (WAIC; McElreath, 2015).

309 **Strategy and Accuracy.** To assess the impact of strategy on performance, we  
310 investigated average accuracies in BASE and PROBE trials. Recall that LS, SS, and DS  
311 responses are each considered correct, only varying in their relative efficiencies. Species,  
312 condition and the interaction of species\*condition were included as fixed effects.

313 **Strategy and Trial Time.** To assess the impact of strategy on efficiency, we  
314 investigated average total trial times for PROBE trials in which subjects used the DS, SS,  
315 or LS. Due to an error in recording baboon response times, this analysis was only  
316 possible for human and chimpanzee data. For each subject, response time outliers  
317 (outside of 1.5 x the inter-quartile range of the first and third quartile) were excluded.  
318 Species, condition and the interaction of species\*condition were included as fixed effects.

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<sup>4</sup> The human participant that preferred to identify as neither male nor female was randomly included as female. However, excluding this participant did not change any results.

319           **Switch Costs.** We also analyzed costs associated with switching between the LS  
320 and the DS. Baboon data were excluded from all switch cost analyses because they  
321 received a different ratio of PROBE:BASE trials (4:1 instead of 1:1). Only subjects who  
322 used the DS in greater than 50% of PROBE trials were included (humans:  $N = 6$ ;  
323 chimpanzees:  $N = 7$ ). Trials that were preceded by an incorrect response were excluded  
324 because it is not possible to assess which strategy was used in incorrect trials.

325           **Accuracy.** First, we compared subjects' Response 1 accuracies between trials in  
326 which the condition repeated or was different. For example, a PROBE trial preceded by  
327 another PROBE trial would be classified as condition = PROBE and trial type = *repeat*,  
328 and a PROBE trial preceded by a BASE trial would be classified as condition = PROBE  
329 and trial type = *different*. Species, condition, trial type and their interactions were  
330 included as fixed effects.

331           **Response Time.** Second, we determined the first response time (RT1) for each  
332 trial, by isolating the time between the fixation response and the first response. All trials  
333 in which the first response was incorrect, or did not correspond to either LS or DS  
334 strategies were excluded. Additionally, for each subject, response time outliers (outside  
335 of 1.5 x the inter-quartile range of the first and third quartile) were excluded. For each  
336 trial, subjects' strategy choice in relation to their previous strategy choice was  
337 determined. For example, if a PROBE trial wherein the subject used the DS was preceded  
338 by another PROBE trial wherein the subject had used the DS, this would be classified as  
339 condition = PROBE and shift type = *stay*, and if a PROBE trial wherein the subject used  
340 the DS was preceded by a BASE trial wherein the subject had used the LS, this would be  
341 classified as condition = PROBE and shift type = *switch*.

342

343

## Results

### 344 Training Phase

345 **Training and Species.** Chimpanzees' training required an of 295.8 days (range:  
346 27-465 days). Across all training levels, chimpanzees required significantly more training  
347 trials than baboons, which required significantly more training trials than humans [ $\chi^2(2) =$   
348 8.61,  $p = 0.014$ ; Table 2].

349 **Training Errors.** To better understand the immense number of training trials that  
350 chimpanzees and baboons needed to learn the LS, we analyzed for error patterns during  
351 Training 2. We chose to analyze Training 2 errors because, unlike Training 1, subjects  
352 selected between all four response options and even by Training 3, chimpanzees' and  
353 baboons' (but not humans') Response 1 (chimpanzees:  $M = 69.3\%$ , baboons: 74.1%) and  
354 Response 2 (chimpanzees:  $M = 65.7\%$ , baboons: 85.5%) accuracies were significantly  
355 lower than Response 3 [(chimpanzees:  $M = 93.5\%$ , baboons: 88.7%);  $\chi^2(4) = 2626.4$ ,  $p <$   
356 0.001; Figure S2]. Thus, chimpanzee and baboon subjects' difficulty learning the LS  
357 involved their representation of the Square1  $\rightarrow$  Square2 portion of the solution, not the use  
358 of the Triangle.

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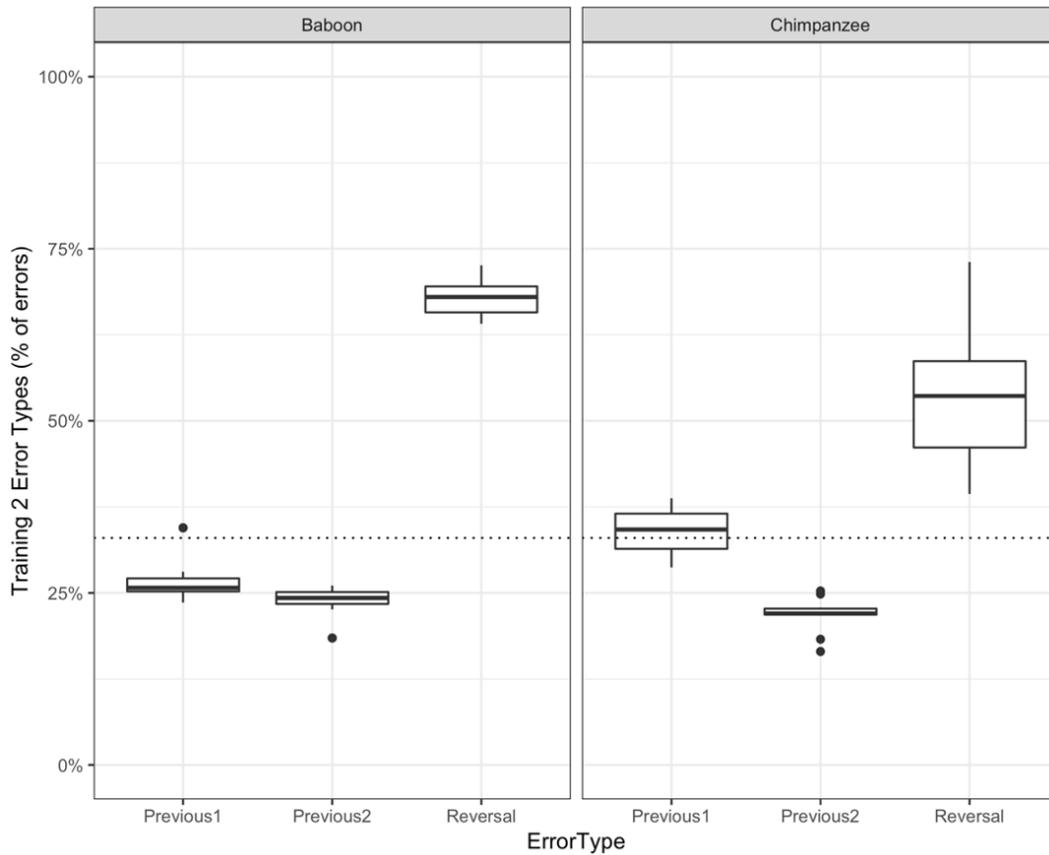
**Table 2.** Median, Interquartile Range (IQR) for the Number of Training Trials Required for All Species

	Baboons	Chimpanzees	Humans
<b>Training 1</b>	<b>6084</b> (4794-6650)	<b>817</b> (310-1362)	<b>8</b> (8-16)
<b>Training 1.5</b>	-----	<b>2343</b> (980-3099)	-----
<b>Training 2</b>	<b>6108</b> (4167-7456)	<b>8771</b> (8283-10276)	<b>8</b> (8-8)
<b>Training 3</b>	<b>2133</b> (2016-2294)	<b>4852</b> (3260-11531)	<b>8</b> (8-16)
<b>Total</b>	<b>14235</b> (11767-16544)	<b>17960</b> (14776-25284)	<b>32</b> (24-48)

365

366 For chimpanzees, Previous1 errors did not significantly differ from chance ( $M =$   
367 33.9%;  $t(9) = 0.80, p = .442, d = .25$ ), Previous2 errors occurred significantly less often  
368 than expected by chance ( $M = 21.8%$ ;  $t(9) = -13.36, p < .001, d = 4.22$ ), and Reversal  
369 errors occurred significantly more often than chance ( $M = 53.6%$ ;  $t(9) = 6.64, p < .001, d$   
370  $= 2.10$ ; Figure 2b). For baboons, Previous1 errors occurred significantly less often than  
371 expected by chance ( $M = 26.5%$ ;  $t(14) = -10.06, p < .001, d = 2.60$ ), Previous2 errors  
372 occurred significantly less often than expected by chance ( $M = 24.0%$ ;  $t(14) = -18.63, p <$   
373  $.001, d = 4.81$ ), and Reversal errors occurred significantly more often than chance ( $M =$   
374  $68.0%$ ;  $t(14) = 52.40, p < .001, d = 13.53$ ; Figure 2). Only a small subset of humans ( $N =$   
375 38) committed errors of this type, and those comprised very few trials ( $M \pm SD$ :  
376 Previous1 =  $2.58 \pm 4.67$  trials, Previous2 =  $2.14 \pm 4.50$  trials, Reversal =  $4.51 \pm 6.35$   
377 trials). Thus, human Training 2 errors were not eligible for further analysis.

378



379

380 **Figure 2.** The median number of trials for each error type in Training 2 (solid horizontal  
 381 line), inter-quartile range (IQR; box), values within 1.5 x IQR (whiskers), and outliers  
 382 (solid circles).

383

### 384 **Experimental Phase**

385 Table 3 reports the percentage of trials in which the Learned, Direct, and Switch  
 386 strategies were used during experimental trials. Strikingly, 15/15 baboons, 6/10  
 387 chimpanzees, and 5/104 humans used the DS the very first time it was available. Indeed,  
 388 baboons used the DS for the first time on *Mdn* trial = 1 (*IQR*: 1-1, *range*: 1-1),  
 389 chimpanzees on *Mdn* trial = 1 (*IQR*: 1-2, *range*: 1-5), and humans on *Mdn* trial = 7 (*IQR*:  
 390 2-17.5, *range*: 1-44). In fact, 8/10 baboon and 2/10 chimpanzee subjects used the DS in

391 every single PROBE trial. In contrast, baboons used the SS for the first time on *Mdn* trial  
 392 = 18 (*IQR*: 10.8-38%, *range*: 3-47%), chimpanzees on *Mdn* trial = 1.5 (*IQR*: 1-5.75%,  
 393 *range*: 1-10%), and humans on *Mdn* trial = 14 (*IQR*: 8-22.2%, *range*: 3-46%).  
 394

**Table 3.** Median, Interquartile Range (*IQR*), and Range Values for the Percentage of Trials in Which Learned, Direct, and Switch Strategies Were Used in BASE and PROBE Trials for All Species.

Note. LS = learned strategy; DS = direct strategy; SS = switch strategy. There was no difference in shortcut use between chimpanzees who received the brief Training 3 modification (N = 5; Mdn = 54.2%) and those who did not (N = 5; Mdn = 60.4%).

		Baboons		Chimpanzees		Humans	
BASE	LS	89.60%		66.70%		91.70%	
		<i>IQR</i> : 80.2-90.6	<i>range</i> : 68.8-97.9	<i>IQR</i> : 65.1-70.3	<i>range</i> : 56.2-77.1	<i>IQR</i> : 85.4-97.9	<i>range</i> : 52.1-100
	DS	0%		2.10%		0%	
		<i>IQR</i> : 0-0	<i>range</i> : 0-2.1	<i>IQR</i> : 0-2.1	<i>range</i> : 0-6.3	<i>IQR</i> : 0-0	<i>range</i> : 0-8.3
PROBE	SS	0%		7.30%		0%	
		<i>IQR</i> : 0-1.0	<i>range</i> : 0-4.2	<i>IQR</i> : 4.7-9.9	<i>range</i> : 2.1-12.5	<i>IQR</i> : 0-0	<i>range</i> : 0-2.1
	LS	0%		10.40%		89.60%	
		<i>IQR</i> : 0-0	<i>range</i> : 0-2.1	<i>IQR</i> : 0.5-16.1	<i>range</i> : 0-27	<i>IQR</i> : 79.2-95.8	<i>range</i> : 4.8-100
PROBE	DS	97.90%		57.30%		0%	
		<i>IQR</i> : 94.8-100	<i>range</i> : 89.6-100	<i>IQR</i> : 41.7-80.2	<i>range</i> : 22.9-100	<i>IQR</i> : 0-0	<i>range</i> : 0-85.4
	SS	0%		17.70%		0%	
	<i>IQR</i> : 0-2.1	<i>range</i> : 0-8.3	<i>IQR</i> : 7.8-28.6	<i>range</i> : 0-50	<i>IQR</i> : 0-2.1	<i>range</i> : 0-16.7	

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403 **Strategy-Use Models.** Table 4 reports the parameter estimates for all models.  
 404 Model 2 had the lowest WAIC, and a weight of 1, suggesting the best out-of-sample fit;  
 405 we interpret only Model 2 in what follows.  
 406

**Table 4.**  $M \pm SE$  parameter estimates for Model 0, Model 1, and Model 2.

*Note.* LS = learned strategy; SS = switch strategy; DS = direct strategy; WAIC = widely applicable information criteria. Reference categories are LS (strategy), Baboon (species), BASE (condition), and Male (sex). Estimates whose 95% credible intervals did not include zero are bolded.

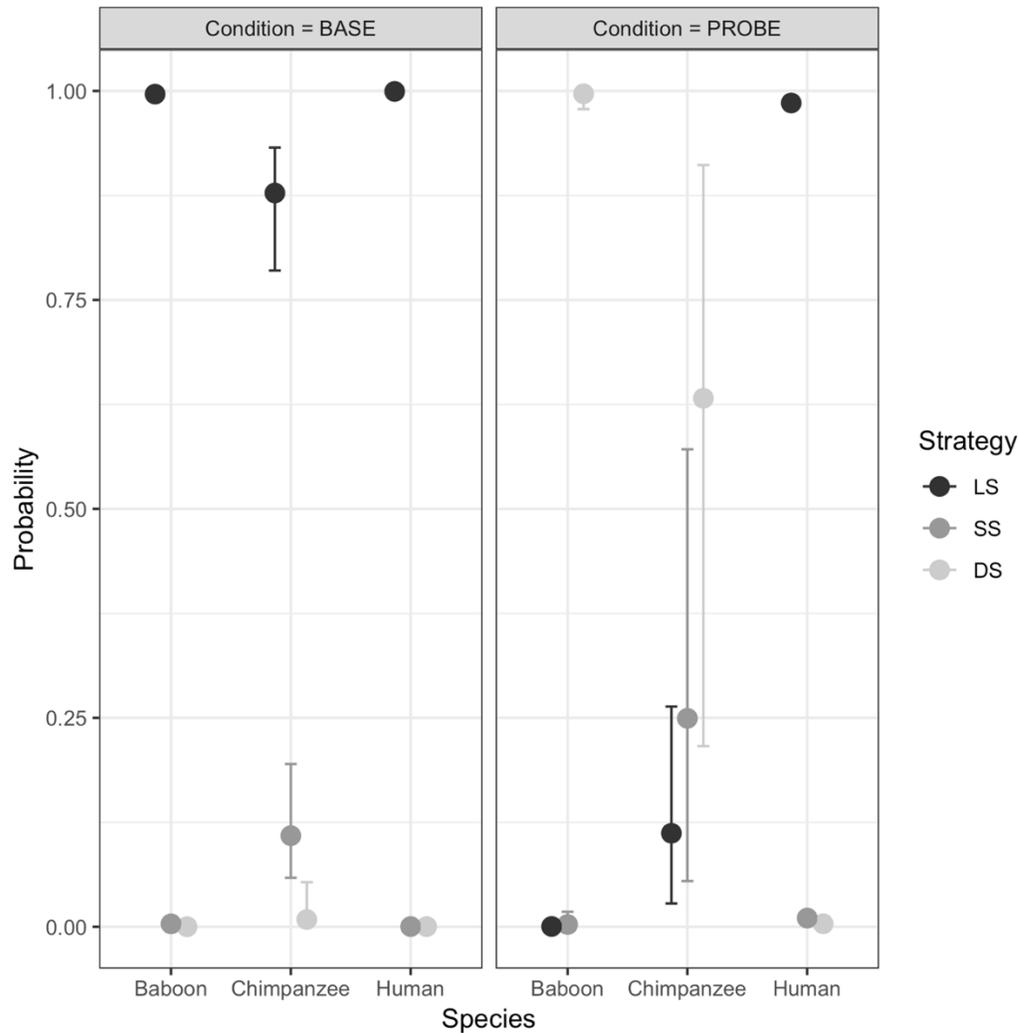
Effects	LS vs. SS	LS vs. DS
<i>Model 0; WAIC = 5523.74 ± 123.01</i>		
Intercept	<b>-5.31 ± .29</b>	<b>-4.93 ± .43</b>
<i>Model 1; WAIC = 3008.76 ± 147.50</i>		
Intercept	<b>-4.77 ± .42</b>	<b>-3.37 ± .74</b>
Species – Baboon vs. Chimpanzee	<b>3.14 ± .53</b>	-0.87 ± 1.10
Species – Baboon vs. Human	<b>-2.33 ± .42</b>	<b>-8.11 ± .80</b>
Condition – BASE vs. PROBE	<b>3.05 ± .23</b>	<b>6.37 ± .23</b>
Age	<b>-0.04 ± .01</b>	-0.01 ± .02
Total Training	0.09 ± .13	0.37 ± .26
Sex – Male vs. Female	-0.05 ± .27	0.37 ± .56
<i>Model 2; WAIC = 2795.38 ± 126.32</i>		
Intercept	<b>-5.18 ± .55</b>	<b>-9.72 ± 1.90</b>
Species – Baboon vs. Chimpanzee	<b>3.59 ± .65</b>	<b>5.31 ± 2.11</b>
Species – Baboon vs. Human	<b>-2.58 ± .96</b>	1.37 ± 1.85
Condition – BASE vs. PROBE	<b>7.86 ± 1.45</b>	<b>18.04 ± 2.37</b>
Age	<b>-0.04 ± .01</b>	-0.01 ± .02
Total Training	0.09 ± .13	0.37 ± .28
Sex – Male vs. Female	0.05 ± .27	0.53 ± .60
Species*Condition		
Baboon vs. Chimpanzee, BASE vs. PROBE	<b>-4.99 ± 1.48</b>	<b>-11.70 ± 2.42</b>
Baboon vs. Human, BASE vs. PROBE	<b>-4.17 ± 1.67</b>	<b>-15.10 ± 2.37</b>

407  
 408 Number of training trials and sex were not strong predictors for using either the  
 409 SS or DS. Age was a strong predictor of SS-use, but the effect was small; with every one-  
 410 year increased in age, subjects were 1.04 (risk ratio =  $1/e^{-.04}$ ) times less likely to select SS  
 411 compared to the LS. Age was not a strong predictor for DS-use. We did not test for a  
 412 three-way interaction between species, condition and age because of the large differences

413 in ages-sampled across species; however, our previous report noted an age-effect on  
414 shortcut-use in humans wherein children under age 11 were more likely to be classified  
415 as shortcut-users than adolescents (12-17) or adults (18+; Pope et al., 2015).

416         There was a strong effect of the interaction between species and condition on SS-  
417 and DS-use. Figure 3 shows this interaction; in BASE trials, the probabilities of using the  
418 SS and the DS were lower than LS-use for all species; however, chimpanzees exhibited  
419 more SS-use compared with humans and baboons. In PROBE trials, baboons exhibited an  
420 enhanced likelihood of using the DS, compared to both other species. Humans exhibited  
421 an enhanced likelihood of using the LS, compared to both other species. However,  
422 chimpanzees exhibited an inconsistent probability of using all three strategies. Indeed,  
423 when considering *Mdn* strategy-use for each subject's PROBE trials, most baboons and  
424 humans consistently selected either LS or DS strategies, whereas chimpanzees showed a  
425 much more varied response pattern (Figure S3).

426



427

428 **Figure 3.** The relative probabilities of selecting the LS, SS, and DS in BASE and PROBE  
 429 conditions, across species. Error bars indicate 95% credible intervals.

430

431 **Strategy and Accuracy.** We found a significant interaction between species and  
 432 condition on accuracy ( $\chi^2(2) = 117.4, p < .001$ ). For baboons, PROBE ( $M \pm SD = 98.2 \pm$   
 433 2.1%) accuracy was significantly higher than BASE ( $M \pm SD = 86.2 \pm 8.8%$ ) accuracy  
 434 ( $Z = -4.18, p < .001$ ). Similarly, for chimpanzees, PROBE ( $M \pm SD = 90.4 \pm 10.2%$ )  
 435 accuracy was significantly higher than BASE ( $M \pm SD = 77.1 \pm 5.0%$ ) accuracy ( $Z = -$   
 436 3.76,  $p < .001$ ). But for humans, BASE ( $M \pm SD = 90.6 \pm 9.8%$ ) accuracy was

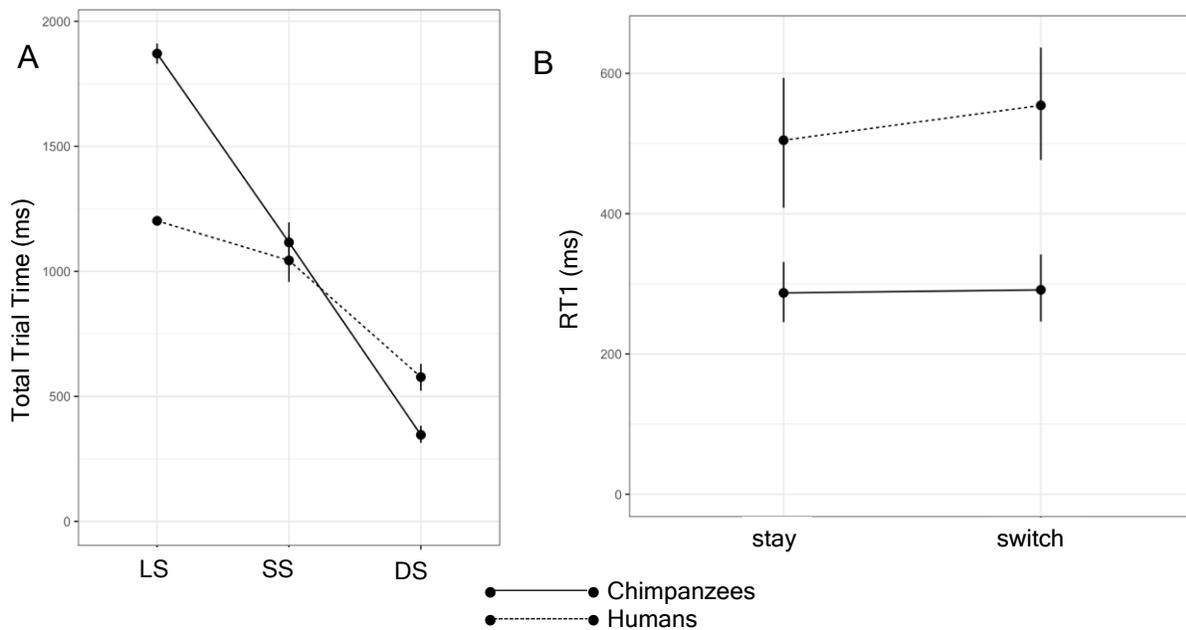
437 significantly higher than PROBE ( $M \pm SD$ : = 88.8  $\pm$  11.1%) accuracy ( $Z = 2.78$ ,  $p =$   
438 .005), indicating that although they typically did not use the DS, the presence of the  
439 triangle in PROBE trials may have been distracting for humans.

440 **Strategy and Total Trial Time.** We found a significant interaction effect of  
441 species\*strategy ( $\chi^2(2) = 276.7$ ,  $p < .001$ ; Figure 4A). For chimpanzees, DS ( $M \pm SD$ : =  
442 346  $\pm$  304ms) total trial times were significantly faster than SS ( $M \pm SD = 1116 \pm 468$ ms;  
443  $t(120.1) = 12.71$ ,  $p < .001$ ) total trial times, which were significantly faster than LS ( $M \pm$   
444  $SD = 1871 \pm 414$ ms;  $t(129.0) = 12.75$ ,  $p < .001$ ) total trial times. For humans, DS ( $M \pm$   
445  $SD$ : = 577  $\pm$  420ms;  $t(112.3) = 18.06$ ,  $p < .001$ ) and SS ( $M \pm SD = 1044 \pm 355$ ms;  
446  $t(871.6) = 2.38$ ,  $p = .046$ ) total trial times were significantly faster than LS ( $M \pm SD =$   
447 1202  $\pm$  398ms) total trial times. Finally, humans' DS total trial times were significantly  
448 slower than chimpanzees' ( $t(112.3) = 6.89$ ,  $p < .001$ ) and humans' LS total trial times  
449 were significantly faster than chimpanzees' ( $t(129.0) = -2.33$ ,  $p = .021$ ).

450 **Switch Costs.**

451 **Accuracy.** We found no significant main or interaction effects of species ( $\chi^2(1) =$   
452 2.68,  $p = 0.102$ ) or trial type (repeat and different;  $\chi^2(1) = .215$ ,  $p = 0.643$ ) on Response 1  
453 accuracies.

454 **Response Time.** We found a significant interaction between species and shift type  
455 (stay and switch;  $\chi^2(4) = 3.85$ ,  $p = 0.050$ ), wherein humans but not chimpanzees took  
456 significantly longer to start responding when switching between LS and DS strategies ( $t =$   
457 2.81,  $p = .012$ ; Figure 4B).



459 **Figure 4.** A) Total trial times by LS, SS, and DS. B) RT1(ms) by shift type.

460

461

### 461 Discussion

462 The current study found that chimpanzees exhibited an intermediate susceptibility  
 463 to cognitive set on the LS-DS task. Their shortcut-use broadly resembled baboons', in  
 464 that it was far greater than that of humans. However, as evidenced by their increased  
 465 inter-individual variation in strategy selection as well as their use of the SS, chimpanzees'  
 466 response style was still influenced by their learned strategy to some extent. These results  
 467 contradict some existing reports of inflexibility in chimpanzees; however, we suggest that  
 468 this is due to methodological differences.

469

### 470 Implications for Optional-Switch Cognitive Flexibility in Chimpanzees

471 First, a portion of the social learning studies reporting inflexibility in apes may have

472 inadvertently extinguished the alternative strategy during training by ‘locking’ it or  
473 rendering it ineffective (Davis et al., 2018, 2016; Manrique & Call, 2015; Price et al.,  
474 2009). This is important because if subjects attempt to use the alternative during training  
475 (the reason it is locked) and are met with failure, subsequent avoidance of the alternative  
476 solution could just be a product of their previously unrewarding experience with that  
477 strategy (i.e. it did not work), resulting in their using it less than naïve controls. By  
478 design, the LS-DS task is meant to promote shortcut use in PROBE trials. The DS is  
479 highly salient and does not rely on working memory; once the triangle appears it remains  
480 on the screen alongside three white squares, until it is selected (either before or after  
481 Squares 1 and 2). Furthermore, the triangle is very familiar and highly associated with  
482 reward; every time it is selected, throughout Training 3 and the experimental trials (both  
483 BASE and PROBE), subjects receive a reward. Clearly, subjects of all species that used  
484 the shortcut the first time it was available (baboons  $N = 15/15$ , chimpanzees  $N = 6/10$ ,  
485 humans  $N = 5/104$ ) directly associated the triangle with the reward.<sup>5</sup> Given the task  
486 design, it is not surprising when subjects, of any species, prefer the DS. What is  
487 remarkable is humans’ robust proclivity for the relatively inefficient LS.

488         Second, as mentioned previously, many social learning studies rely on a model to  
489 demonstrate the more efficient alternative (Davis et al., 2018, 2016; Dean, Kendal,  
490 Schapiro, Thierry, & Laland, 2012; Gruber et al., 2011; Hanus, Mendes, Tennie, & Call,  
491 2011; Hrubesch et al., 2009; Marshall-Pescini & Whiten, 2008; Price et al., 2009),

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<sup>5</sup> As mentioned, half of the chimpanzee subjects avoided selecting the triangle when it first appeared in Training 3 (one subject even ran away from the touch screen the very first time it appeared), only selecting it when a modified version of the task removed all other options. This further suggests that chimpanzees’ flexibility on the LS-DS task was reliant upon their familiarity with the triangle. Davis et al. (2018) reported similarly enhanced behavioral flexibility when an alternative strategy for opening a puzzle box was simple and involved a familiar motor action.

492 introducing the possibility that perseveration may not be derived from cognitive  
493 inflexibility but from a failure to extract the relevant information from (or even attend to)  
494 the demonstration. In the LS-DS task, subjects are not shown how to enact the shortcut. It  
495 is an already familiar step in their previously learned solution and is therefore not  
496 confounded by social learning ability.

497 Finally, some tasks that describe conservative behavior in chimpanzees state that  
498 the behavior is clearly within the species' repertoire (Marshall-Pescini & Whiten, 2008)  
499 and thus, would be readily utilized if subjects were not influenced by a more familiar  
500 solution. However, what may be present in the species' repertoire is not necessarily  
501 present within the individual's and inexperience with specific manipulations, especially  
502 those involving fine motor control or tool-use, should not be discounted (Dean et al.,  
503 2012; Gruber et al., 2011). The time spent learning how to perform the seemingly more  
504 efficient alternative may easily render it less so. By comparison, the LS, DS, and SS  
505 strategies enlist motorically identical actions. Our findings demonstrate that, under  
506 certain conditions, chimpanzees are capable of flexibly switching between abstract  
507 response strategies. However, the extent to which this carries over into more naturalistic  
508 contexts should be elucidated in future endeavors.

509

### 510 **Species Differences in Cognitive Set on the LS-DS Task**

511 Why are humans but not baboons nor (to a large extent) chimpanzees, affected by  
512 cognitive set in the LS-DS task? Thousands more training trials were needed for  
513 chimpanzees (range: 2,784-36,966) and baboons (range: 5,043-20,060) to learn the LS,  
514 compared with humans (range: 24-152). We suggest that LS-use may be aided by

515 humans' enhanced ability to learn rules, either through verbal encoding (Ghirlanda, Lind,  
516 & Enquist, 2017), heightened working memory (Fagot & De Lillo, 2011; but see Inoue &  
517 Matsuzawa, 2007), or chunking strategies (Gobet et al., 2001; Kolodny, Edelman, &  
518 Lotem, 2015). In fact, many of the human subjects were able to learn the rule after only 8  
519 trials – a quarter of the total possible configurations – illustrating that, once learned,  
520 humans are capable of accurately applying the LS to novel situations (Pope et al., 2015).  
521 On the other hand, chimpanzees and baboons required many encounters with the same  
522 trial configurations before they began to accurately respond. When examined,  
523 chimpanzees' and baboons' errors seem to have been driven, to a large extent, by  
524 erroneously reversing the order of the demonstrated squares (i.e. selecting Square2 first).  
525 This reversal error is in line with recent findings which suggest that humans exhibit a  
526 pronounced advantage when it comes to sequential encoding (Ghirlanda et al., 2017).  
527 Indeed, a less firmly encoded LS could conceivably facilitate baboons' and chimpanzees'  
528 ability to replace it.

529       It is also possible that increased DS-use might result from failure to inhibit the  
530 triangle response, which during the final training level is most closely associated with  
531 reward. Indeed, baboons' and chimpanzees' propensity for reversal errors during the  
532 training phase seems to support this notion. However, if failure to inhibit were driving  
533 shortcut-use in PROBE trials, we would expect similar inhibitory failures to trigger  
534 erroneous BASE responses. Yet there were no significant differences between species'  
535 Response 1 (Square 1) accuracies in BASE trials (Figure S4). Thus, although it is  
536 plausible that baboons' and chimpanzees' training phase reversal errors were a function  
537 of inhibitory failure, it does not appear to have driven species differences in strategy-use

538 during the experimental phase.

539       The current study found that chimpanzees, unlike humans (Pope et al., 2018), did  
540 not exhibit switch costs on the LS-DS task. As far as we are aware, this is the first study  
541 to investigate deficits associated with switching between abstract rules in chimpanzees.  
542 Stoet & Snyder (2003) posited that switch costs are a product of firmly encoded rules,  
543 such that greater cognitive effort is required to suppress the previous strategy and activate  
544 the current. Additionally, less entrenched rules have been hypothesized to amplify  
545 distractibility (Stoet & Snyder, 2008), which for the LS-DS task might further promote  
546 the use of the shortcut.

547       That said, chimpanzees, but not baboons, utilized the SS, suggesting that  
548 chimpanzees may have been influenced by their familiarity with the LS, at least to some  
549 extent. We posit that differences in how baboons and chimpanzees process sequences  
550 might have affected their relative abilities to separate the shortcut from the sequence as a  
551 whole. When identifying components of a sequence, baboons have been shown to find  
552 and select each component in turn, yet chimpanzees and humans appeared to identify the  
553 entire sequence first, only then proceeding to make the appropriate selections (Kawai &  
554 Matsuzawa, 200AD; Ohshiba, 1997). Chimpanzees may exhibit intermediate  
555 susceptibility to cognitive set on the LS-DS task because, unlike humans, they are not  
556 verbally encoding their solution strategy and, unlike baboons, they are processing the  
557 sequence more holistically (however, see Beran, Pate, Washburn, & Rumbaugh, 2004).

558       Our findings are also in line with the overimitation literature which shows that,  
559 compared to humans, chimpanzees are much better able to cut out irrelevant portions of a  
560 demonstrated box-opening sequence (Horner & Whiten, 2005; McGuigan, Makinson, &

561 Whiten, 2011; McGuigan, Whiten, Flynn, & Horner, 2007). Future efforts aimed at  
562 disentangling these influences would do well to compare cognitive set between monkeys  
563 and apes using a non-sequential task.

564 We suggest that the distinctive response patterns observed between baboons,  
565 chimpanzees, and human adults on the LS-DS task may be explained by a trade-off  
566 between how quickly abstract rules can be learned and the degree to which they can be  
567 flexibly used, a process potentially governed by differences in strategy-encoding. That  
568 said, we consistently find that some humans both adopt the LS quickly *and* use the DS  
569 (Pope et al., 2015). For example, we recently found population-level differences in  
570 shortcut-use between Western humans (6% used the DS in more than 5% of trials) and  
571 the seminomadic Himba (35% used the DS in more than 5% of trials; Pope et al., 2018)  
572 suggesting that, at least within humans, propensity toward cognitive set on the LS-DS  
573 task may vary by culture. Yet, although 100% of the tested chimpanzees and baboons  
574 used the DS in more than 5% of trials, the highest proportion of humans to be classified  
575 as DSers so far is 69% (Pope, Washburn, & Hopkins, submitted), which occurred after  
576 subjects watched a video demonstrating the shortcut.<sup>6</sup>

577

### 578 **Concluding Remarks**

579 Adaptive behavior requires a balance between flexible and perseverative response  
580 strategies. On one hand, if a familiar strategy is too concrete it may be unresponsive to  
581 changing contextual cues, leading to an inefficient or even maladaptive response. On the

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<sup>6</sup> Note: 31% of human adults that watched a video of the shortcut and still did not use it in subsequent trials.

582 other hand, if strategies are too malleable, then responses may be crippled by irrelevant or  
583 even erroneous information (Cools, 2008; Hommel & Colzato, 2017; Roberts, 2008).  
584 Cognitive flexibility is a multifaceted construct that should be measured in both forced-  
585 switch and optional-switch contexts. Although humans outperform non-human primates  
586 in forced-switch contexts, the current study found that, within an optional-switch context,  
587 chimpanzees exhibited an intermediary susceptibility to cognitive set compared with  
588 baboons, who easily adopted the shortcut, and humans, who became stuck on the familiar  
589 but relatively inefficient learned strategy. Future investigations into how the various  
590 aspects of cognitive flexibility vary within individuals and between primate species must  
591 necessarily include optional-switch metrics.

592

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