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2 Action-matching biases in monkeys (*Sapajus spp.*) in a stimulus-response compatibility task:

3 Evaluating experience-dependent malleability

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## Abstract

20 Stimulus-response compatibility effects occur when observing certain stimuli facilitate the  
21 performance of a related response and interfere with performing an incompatible or different  
22 response. Using stimulus-response action pairings, this phenomenon has been used to study  
23 imitation effects in humans, and here we use a similar procedure to examine imitative biases  
24 in non-human primates. Eight capuchin monkeys (*Sapajus spp.*) were trained to perform hand  
25 and mouth actions in a stimulus-response compatibility task. Monkeys rewarded for  
26 performing a compatible action (i.e., using their hand or mouth to perform an action after  
27 observing an experimenter use the same effector) performed significantly better than those  
28 rewarded for incompatible actions (i.e., performing an action after observing an experimenter  
29 use the other effector), suggesting an initial bias for imitative action over an incompatible S-R  
30 pairing. After a predetermined number of trials, reward contingencies were reversed; i.e.,  
31 monkeys initially rewarded for compatible responses were now rewarded for incompatible  
32 responses, and vice versa. In this second training stage no difference in performance was  
33 identified between monkeys rewarded for compatible or incompatible actions, suggesting any  
34 imitative biases were now absent. In a second experiment, two monkeys learned both  
35 compatible and incompatible reward contingencies in a series of learning reversals. Overall, no  
36 difference in performance ability could be attributed to the type of rule  
37 (compatible/incompatible) being rewarded. Together, these results suggest that monkeys  
38 exhibit a weak bias towards action copying, which (in line with findings from humans) can  
39 largely be eliminated through counter-imitative experience.

40 *Keywords:* stimulus-response compatibility, imitation, social learning, capuchin monkeys.

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43 Evaluating experience-dependent malleability

44 To imitate, an animal may recreate, through action, the perceived visual qualities of the  
45 act they see performed by another. However, the visual information obtained from perceiving  
46 another animal's actions often does not correspond to the sensory experience of observing  
47 one's own performance of the same action; indeed, sometimes an action is entirely opaque to  
48 the actor (e.g., when performing a facial expression). The cognitive challenge in overcoming  
49 this so-called correspondence problem (Nehaniv & Dautenhahn, 2002) might explain why  
50 researchers examining action imitation (more specifically defined as converting "visual  
51 information into matching motor acts", Custance, Whiten, & Fredman, 1999, p. 14), in  
52 nonhuman primates, have concluded that there is a qualitative difference in comparison with  
53 human abilities (Call & Tomasello, 1995; Fragaszy, Deputte, Cooper, Colbert-White, &  
54 Hémery, 2011; Subiaul, 2016; Tennie, Call, & Tomasello, 2012; Tomasello, Davis-Dasilva,  
55 Camak, & Bard, 1987). Indeed, the question of imitative ability in animals dates to early work  
56 in the comparative tradition (Thorndike, 1911), and has continued in more recent times  
57 (Caldwell & Whiten, 2002), however, even those who claim nonhuman apes might possess  
58 some capacity to imitate are more cautious when describing the abilities of monkeys (Whiten  
59 & van de Waal, in press).

60 Over the last decades, researchers of social learning have documented many failed  
61 attempts to observe action imitation in monkeys (e.g., Fragaszy et al., 2011; for reviews see  
62 Fragaszy & Visalberghi, 2004; Visalberghi & Fragaszy, 2001), yet studies using simple,  
63 extractive foraging tasks have provided some evidence that monkeys will match the body part  
64 used by a conspecific to open containers. Voelkl and Huber (2000) found that common  
65 marmosets (*Callithrix jacchus*) were more likely to open a box with their hand after observing

66 a conspecific use the same body-part, when compared to individuals who had seen the container  
67 opened by mouth. Furthermore, a detailed frame-by-frame analysis of the video footage of  
68 these actions found that specific action characteristics measured when the monkeys opened the  
69 box with their mouth (e.g., head inclination) were significantly more alike when one monkey  
70 had watched another perform the action (in comparison to monkeys who had not observed a  
71 conspecific; Voelkl & Huber, 2007). Using a similar methodology with a larger sample of  
72 vervet monkeys (*Chlorocebus aethiops*), van de Waal and Whiten (2012) provided further  
73 evidence of body-part matching. Subjects were more likely to use their hand after observing a  
74 conspecific use that same action when opening a food-baited canister. These studies of bodily  
75 imitation in a few species of monkeys provide the extent of positive findings on motor imitation  
76 in adult monkeys, although evidence of a distinctive form of imitative behavior, which may be  
77 unrelated to the current question of imitation in adult monkeys, has also been reported in  
78 neonates (e.g., Ferrari et al., 2006).

79         Developmental approaches to imitation suggest certain types of experience are crucial  
80 for imitative ability to develop. For example, the associative sequence learning approach and  
81 ideomotor approach posit that imitative ability is formed through compatible sensorimotor  
82 experience; i.e., the contingent experience of performing and observing the same action  
83 (Heyes, 2010; Heyes & Ray, 2000; Prinz, 1997, 2005). This sensorimotor experience could  
84 occur when an infant observes their own actions or by being imitated by caregivers (Del  
85 Giudice, Manera, & Keysers, 2009). Support for experiential accounts of imitation has been  
86 provided through the use of stimulus-response compatibility (SRC) procedures that incorporate  
87 stimulus-response action pairs. With human adults, an action SRC task requires participants to  
88 perform two different actions (e.g., hand opening/closing) while simultaneously presented with  
89 a task irrelevant image that displays either a compatible action (i.e., the action they must  
90 perform) or an incompatible action (i.e., the different action). Reaction times (RTs) are

91 consistently quicker when the image presented corresponds with the action to be performed,  
92 while images of incompatible actions invoke slower responses, a phenomenon described as  
93 automatic imitation (Brass, Bekkering, & Prinz, 2001; Brass, Bekkering, Wohlschläger, &  
94 Prinz, 2000; Heyes, Bird, Johnson, & Haggard, 2005; Stürmer, Aschersleben, & Prinz, 2000).  
95 This action-specific SRC effect is similar to those found in traditional SRC procedures, where  
96 stimuli-response pairs share other overlapping characteristics (e.g., spatial location, Simon &  
97 Rudell, 1967; or semantic content, e.g., Stroop, 1935; for a review see Kornblum, Hasbroucq,  
98 & Osman, 1990), and has been proposed as a method of studying imitation, mimicry, and  
99 mirror neurons in humans (Heyes, 2011).

100         If some forms of imitation are modulated by sensorimotor experience, it follows that  
101 these imitation effects are malleable and should be influenced by sensorimotor training; indeed,  
102 incompatible training sessions, where participants were required to open their hand after seeing  
103 a hand close and vice versa, delivered 24 hours before an action SRC task has been found to  
104 significantly reduce compatibility effects in adult humans (Heyes et al., 2005). Catmur et al.  
105 (2008) used a similar method to examine activity in brain regions associated with mirror neuron  
106 activity, and after incompatible training (performing hand actions when presented with an  
107 image of a foot and vice versa), brain areas previously related with hand actions were active  
108 when viewing images of a foot, possibly suggesting that the neural substrates thought to  
109 facilitate imitative behavior (Gallese, Fadiga, Fogassi, & Rizzolatti, 1996; Iacoboni et al.,  
110 1999), are sensitive to experience. This evidence suggests that existing cognitive relationships  
111 between sensory-motor representations, whether innate or learned, are plastic, and can adapt to  
112 varied inputs. While a nativist and empiricist approaches to imitation are not necessarily  
113 mutually exclusive, a proper understanding of the impact of experience on imitation in

114 nonhuman primates is currently lacking, which presents a stark contrast with the efforts  
115 devoted to investigating pre-existing abilities.

116 With human participants, SRC effects identified using action S-R pairings are examined  
117 using reaction time measurements. They occur when participants (required to perform specific  
118 responses), are unintentionally and automatically influenced by action stimuli in accordance  
119 with the compatibility state of the S-R pairing (Brass et al., 2000; Catmur & Heyes, 2011;  
120 Stürmer et al., 2000). Compatible S-R pairings therefore typically facilitate performance (fast  
121 RTs), whereas incompatible pairings tend to produce interference (slower RTs).

122 Studies that have examined this SRC effect in nonhuman animals follow a different  
123 approach (Mui, Haselgrove, Pearce, & Heyes, 2008; Range, Huber, & Heyes, 2011). Instead  
124 of examining RT response, subjects are trained to respond with two different actions  
125 discriminatively to two action stimuli, and associations between stimuli and responses are  
126 learned by trial and error. Learning success is then compared between compatible (i.e.,  
127 rewarded for performing the action they see) and incompatible S-R pairings (i.e., rewarded for  
128 performing a different action to the one they see), and if compatible pairings are learned more  
129 quickly than incompatible pairings, it is inferred that the perceptual qualities of the action  
130 stimulus aids in the performance of that same action over a different action, indicative of some  
131 imitative ability or bias. Given the training procedure, it is less clear that the compatibility  
132 effects can be said to be “automatic” and so the term automatic imitation may be less suited to  
133 these findings (although to date, the comparative literature has been described using this same  
134 terminology; i.e., Mui et al., 2008; Range et al., 2011).

135 Using this comparative methodology, budgerigars (*Melopsittacus undulates*) rewarded  
136 for imitating a conspecific perform a foot versus a beak action have been found to learn the  
137 associative rule more quickly than subjects rewarded for performing an opposite action (Mui

138 et al., 2008). Similarly, domestic dogs (*Canis lupus familiaris*) rewarded for opening a door  
139 with the same body part as their owner (hand/paw or mouth), learned this rule faster than those  
140 rewarded for using the opposite body part (Range et al., 2011). Furthermore, in the study of  
141 imitative biases in dogs, it was found that once the animals were reinforced for incompatible  
142 rules, their subsequent performance on compatible actions was poorer when compared to dogs  
143 that had not experienced incompatible training. The authors concluded that this suggests that  
144 previous incompatible experience carried over into the subsequent condition where only  
145 imitation was rewarded, which is consistent with experiential accounts of imitative ability. The  
146 use of these learning procedures provides a method of assessing whether S-R associations  
147 relevant to bodily imitation are facilitated by compatibility effects, thus providing a means by  
148 which underlying biases can potentially be revealed.

149         Here, our aims are two-fold. Firstly, using an SRC paradigm, we will examine if  
150 capuchin monkeys find compatible S-R actions pairings (i.e., when hand actions are rewarded  
151 following presentation of a hand-action stimulus, and mouth actions are rewarded following  
152 presentation of a mouth-action stimulus) easier to learn in comparison to incompatible pairings  
153 (i.e., when hand actions are rewarded following presentation of a mouth-action stimulus and  
154 vice versa). Capuchin monkeys are New World primates that interest researchers of social  
155 learning because of their high brain to body-mass ratio (see Fragaszy, Visalberghi, & Fedigan,  
156 2004), socially tolerant nature (Fragaszy, Feuerstein, & Mitra, 1997), tool use capacities  
157 (Visalberghi, 1993), and evidence of socially learned traditions in wild populations (Perry,  
158 2011). Capuchins have been studied extensively to examine their social learning abilities  
159 (Dindo, Thierry, & Whiten, 2008; Dindo, Whiten, & de Waal, 2009; Fragaszy et al., 2011;  
160 Visalberghi & Addessi, 2001) yet no clear evidence of action imitation has been identified in  
161 this species (e.g., Fragaszy et al., 2011). However, though previous studies suggest capuchin  
162 monkeys learn primarily from non-imitative forms of social learning (Craat, Hardy, &

163 Fragaszy, 2010; Fragaszy et al., 2011; Galloway, Addessi, Fragaszy, & Visalberghi, 2005) the  
164 methodology employed here will permit investigation of more subtle imitative biases.  
165 Secondly, if imitative biases are present in capuchins we hope to examine whether this bias is  
166 resistant to counter-imitative training.

167 In a first experiment we address both of these aims. Capuchin monkeys were rewarded  
168 for performing actions with their hand and mouth discriminatively upon observing an  
169 experimenter perform hand and mouth actions. Half of the monkeys were reinforced for  
170 performing the same action they observed the experimenter perform (i.e., performing hand  
171 actions to hand stimuli; mouth actions to mouth stimuli), and the other monkeys were rewarded  
172 for performing the alternative action. We predicted that if capuchin monkeys enter into this  
173 procedure with some bias to imitate specific motor actions they would perform better when  
174 rewarded for the compatible rule. Following this first set of training, the reinforcement of S-R  
175 contingencies was reversed; i.e., monkeys that were initially rewarded for compatible  
176 responses were rewarded for performing incompatible responses, and vice versa. If capuchin  
177 monkeys possess a strong disposition to imitate (whether learned or innate), it might be  
178 expected that during this reversal-learning stage those learners switching from an incompatible  
179 rule to a compatible rule should perform better than individuals that experience the alternate  
180 reversal.

## 181 **Experiment 1: Two-action stimulus response compatibility task**

### 182 **Methods**

#### 183 **Subjects and research site**

184 Eight capuchin monkeys (*Sapajus spp.*) were tested in experiment one (six males; mean  
185 age at the beginning of the study was 3.9 years,  $SD = 2.0$ ; range = 1.4 - 7.5). All monkeys were

186 housed in one of two mixed-species groups with squirrel monkeys (*Saimiri sciureus*) at the  
187 Living Links to Human Evolution Research Centre at Edinburgh Zoo, Scotland. The monkeys  
188 were never food- or water-deprived, and all rewards offered during research sessions were  
189 supplementary to their diet. Before this experiment took place these capuchins had been studied  
190 on a range of cognitive tasks (e.g., Morton, Lee, & Buchanan-Smith, 2013), however, no  
191 previous study had examined action imitation. Ethical approval was granted by the University  
192 of Stirling Psychology Ethics Committee, and all research took place between February 2011  
193 and June 2012.

#### 194 **Materials**

195         Eight research cubicles arranged in a connected 2X4 matrix act as a corridor between  
196 the monkeys' indoor and outdoor enclosures (each cubicle measures 49.5 cm X 52.1 cm X 51.4  
197 cm). Partitioning slides inserted between cubicles allow monkeys to be separated from their  
198 groupmates for research purposes. The cubicle window (i.e., the Perspex screen orientated  
199 toward the experimenter) included a small opening in its center, allowing juice to be delivered  
200 to the capuchins through a mouthpiece connected to a rubber-tube and syringe. On the bottom  
201 left side of the cubicle window was a hole (3.5cm diameter) through which food rewards were  
202 offered. To shape two disparate actions a modified table tennis paddle was used (see Electronic  
203 Supplementary Material, ESM, Video 1.). Alternate sides were colored black and white to  
204 facilitate color discrimination training. A second target was used during the stimulus response  
205 compatibility (SRC) trials that differed in shape and color (see ESM Video 2). Sessions were  
206 recorded on a Sony Mini DV Digital Video Camera.

#### 207 **Shaping behaviors**

208         For monkeys to take part in SRC trials, two actions employing disparate body parts  
209 were trained: touching the cubicle window with a) their hand and b) their mouth. These specific

210 actions were used as they were considered similar to those used in previous comparative work  
211 (Mui et al., 2008; Range et al., 2011), but also trainable through reinforcement. These actions  
212 are not incompatible in the sense of their performance being mutually exclusive (e.g., opening  
213 versus closing a hand), but the use of disparate body parts is common practice when studying  
214 imitation in primates (e.g., Voelkl & Huber, 2000), as well as stimulus-response compatibility  
215 effects in humans and other animals (Catmur & Heyes, 2011; Gillmeister, Catmur, Liepelt,  
216 Brass, & Heyes, 2008; Mui et al., 2008; Range et al., 2011). The training of both actions took  
217 place concurrently through positive reinforcement of successive approximations of each action.

218         To train each individual to touch the cubicle window with their mouth, diluted fruit  
219 juice (one part juice to two parts water) was delivered from a syringe to the mouthpiece on the  
220 inside of the cubicle. Capuchins learned to bring their mouths to the screen to receive the juice  
221 reward. Next, the experimenter presented the training target ~5cm in front of the window before  
222 the juice was delivered. Once capuchins learned to bring their mouths to the window before  
223 the juice was delivered, the juice reward was replaced with a food reward. In some instances  
224 the monkeys would use their hands to balance themselves against the Perspex screen when  
225 performing the mouth action, but this action was still interpreted as a mouth action as the goal  
226 was to place their mouth against the screen. To train a distinct hand action the training target  
227 was presented to the small hole where food rewards were offered. The target was removed once  
228 touched by the subject's hand and a food reward was offered. Gradually, the target was moved  
229 further from the hole, and the subject, unable to touch the target directly, was rewarded for  
230 touching the window with one or two hands. A monkey was never rewarded for a hand action  
231 if their mouth was also presented to the screen. At this point the learned association between  
232 stimulus and action was spatial in nature (the mouth action cued by the target presented near

233 the center of the window; the hand action cued by the target presented nearer the left of the  
234 window).

### 235 **Color discrimination learning**

236         Once actions had been shaped and were performed reliably to spatial cues the target  
237 was only presented in the center of the window and to be rewarded the capuchin was required  
238 to learn a color association rule (see ESM Video 1). The same target (see ESM Video 1) was  
239 used to cue both actions, but a different colored side was used in each case (i.e., for four  
240 monkeys the black side was always presented when training hand actions and the white side  
241 was always presented during the training of mouth actions; the opposite color/action pairing  
242 was reinforced for the other four monkeys). Only correct responses were rewarded, i.e.,  
243 performing an action that corresponded to a specific color, and if an incorrect response was  
244 performed the experimenter turned his back on the monkey for approximately three seconds, a  
245 form of negative punishment, removing the opportunity to receive further rewards for a short  
246 time-period. Once an individual had performed over 85% correct responses on three  
247 consecutive research sessions (20 trials per session), the monkey began the SRC trials.

### 248 **Stimulus Response Compatibility Trials (SRC)**

249         Upon completion of the color discrimination trials, individuals were transferred into  
250 one of two groups: a compatible condition or incompatible condition. During these stimulus  
251 response compatibility trials, the color stimulus was switched for an action stimulus (i.e.,  
252 instead of seeing a black target or a white target on a given trial, the monkey would see the  
253 experimenter touch a target with either his hand or his mouth). Based on performance in the  
254 initial color discrimination stage, groups were counterbalanced to include equal numbers of  
255 quick discrimination learners (mean number of research sessions before reaching criterion on

256 the color discrimination task was 45.75 for subjects in the compatible condition and 45 for  
257 subjects in the incompatible condition). On each research session we attempted to complete  
258 twenty SRC trials with each monkey, however, monkeys could end the research session by  
259 demonstrating cues to leave and so some sessions included fewer trials. During an SRC trial a  
260 second target (see ESM Video 2) was held in front of the experimenter with his left hand and  
261 touched with either a) his right hand or b) his mouth. The target was then moved to ~5cm in  
262 front of the window. The number of hand and mouth actions performed by the experimenter  
263 was kept equal throughout these sessions, i.e., 10 mouth and 10 hand actions, and the order of  
264 hand and mouth stimuli was pseudorandomized (the maximum number of repeats was one;  
265 e.g., the stimuli performed in half an SRC session might proceed as follows: Hand(H)-  
266 Mouth(M)-H-H-M-H-M-M-H-M). Individuals in the compatible condition were rewarded for  
267 performing actions using the same body part as the experimenter; i.e., if the experimenter  
268 touched the target with his hand, the monkey was rewarded for performing an action with their  
269 hand; and if the target was touched by the experimenter's mouth, the monkey was rewarded  
270 for using their mouth). Individuals in the incompatible condition were rewarded for using the  
271 opposite actions; if the experimenter touched the target with his hand, the monkey was  
272 rewarded for performing an action with their mouth, and vice versa.

273         If an action response was ambiguous (i.e., hand placed against the window on its own,  
274 and quickly replaced with a mouth response), the target was removed by the experimenter and  
275 the trial was repeated. A correct response was rewarded with a food item, and an incorrect  
276 response resulted in the experimenter turning his back on the monkey for approximately three  
277 seconds. Actions were judged to be correct/incorrect by the experimenter during the research  
278 session but all sessions were video recorded for subsequent reliability coding. A random  
279 sample of 550 action responses (6%) were extracted from video recordings and information

280 about the action performed by the experimenter (i.e., action stimulus presented) and trial  
281 outcome (i.e., whether monkey was rewarded) was removed. These actions were re-coded by  
282 the same experimenter that had conducted the experiment, and although this individual was not  
283 naïve of the hypotheses, the removal of contextual cues made it impossible to know whether  
284 an action performed by a monkey was in response to the same action or a different action.  
285 Agreement between the experimenter's decision within the research session and without  
286 contextual information was high ( $Kappa = .97$ ;  $p < .001$ ). Once a predetermined learning  
287 criterion was reached ( $\geq 85\%$  correct responses in three consecutive 20 trial sessions) the reward  
288 contingency was to be reversed. However, only one monkey had reached this criterion before  
289 900 trials, and due to time constraints, monkeys were switched to the opposite condition  
290 regardless of progress after 900 trials, and a further 500 trials were completed by each monkey.  
291 Two monkeys were tested on fewer trials in each condition to examine performance on both  
292 associate rules without the potential confounding effects of overtraining (320 trials in each  
293 condition). As monkeys were free to leave in the middle of sessions and the goal of each session  
294 was to test monkeys with 20 trials, monkeys completed on average 10.4 trials more than the  
295 established cut-off.

296         It is worth noting that throughout this action stimulus stage we continued to conduct  
297 some color discrimination trials to confirm that each subject could still perform both trained  
298 actions discriminately. For example, before performing any SRC trials during a given session,  
299 four color discrimination trials were completed (color discrimination trials were also performed  
300 after the 10th SRC trial and after the 20<sup>th</sup> trial). We continued to reward this already learned  
301 association to encourage participation and to assess an individual's ability to perform both hand  
302 and mouth actions discriminately.

### 303 **Data Analysis**

304       The monkeys' success on each trial was recorded as a binary response variable (either  
305 correct or incorrect). This binary variable was used as the outcome variable in a generalized  
306 linear mixed model (GLMM) with a binomial distribution and logit link function to test specific  
307 hypotheses concerning imitative biases in the SRC paradigm. As each monkey received  
308 multiple trials in each condition, the monkey being tested was included as a random intercept  
309 in the GLMMs. Furthermore, session number (i.e., consecutive blocks of 20 trials) was  
310 included as a random slope in the models. To test hypotheses concerning the persistence of an  
311 imitative effect, a model was created with an interaction included for condition and order of  
312 learning. To describe the contribution of predictor variables to trial success, odds ratios were  
313 calculated by back-transforming the log odds ratios. All statistical tests were conducted with  
314 the R statistics program (R Core Team, 2014) in the Rstudio environment (RStudio Team,  
315 2014). Models were developed using the lme4 package (Bates, Maechler, Bolker, & Walker,  
316 2015), and graphics were created using the ggplot2 package (Wickham, 2009). Monkeys  
317 completed up to 900 trials in the first block of learning, but only the first 500 trials for each  
318 monkey were examined (320 in the case of two monkeys), for two reasons. Firstly, one  
319 monkey's associative rule was switched after 500 trials, so a comparison between groups is  
320 balanced at this point (see ESM, Figures 1 and 2 for all performance data summarized for each  
321 monkey- areas highlighted in light grey were analyzed). Also, to examine any pre-existing bias  
322 in automatic imitative ability it is more appropriate to examine earlier performances.

### 323 **Results**

324       Overall, monkeys were biased towards mouth actions, performing this action in 54.54%  
325 of all analyzed trials. Every monkey developed an effector preference at some stage of the  
326 experiment; i.e., the same action was used consistently across a session. For example, when

327 looking at diversity of action performance, we find that across all monkeys and testing sessions,  
328 on average, 90.9% of responses within a 20-trial session consisted of one type of action  
329 (although this bias could alternate across sessions; e.g., a monkey that performs mainly hand  
330 actions in one session might change to mouth responses on the following session). As trial  
331 success in this context is unlikely to be related to a learned association between a specific  
332 stimulus and response, and as overall success above a 50% chance level requires a diversity of  
333 actions, effector was not examined as a predictor of success.

334 Descriptive data on overall performance for each monkey can be found in Table 1 (also  
335 see ESM, Figures 1 and 2 for all performance data plotted chronologically by session). A  
336 GLMM found a significant interaction between the rule being rewarded  
337 (compatible/incompatible) and the order in which the rule was learned (Wald test,  $\beta$  [condition  
338 x order] = 0.298, s.e. = 0.148,  $z = 2.012$ ,  $p = 0.044$ ; see Table 2 for full model; see Figure 1). In  
339 the first block of discrimination learning the chance of success was significantly lower when  
340 learning an incompatible rule (an estimated 22.81% lower odds of being correct, confidence  
341 intervals, 95% CIs: 1.33% - 39.62%; Wald test,  $\beta$  [incompatible] = -0.259, s.e. = 0.125,  $z = -$   
342 2.067,  $p = .039$ ; see Figure 1 when order = first), but in the second block of learning (i.e., after  
343 associative rules were switched), the type of associative rule being rewarded did not influence  
344 chance of success (Wald test,  $\beta$  [incompatible] = 0.039, s.e. = 0.076,  $z = 0.512$ ,  $p = .608$ , see  
345 Figure 1 when order = second; estimated 3.99% greater odds of success on an incompatible  
346 trial, CIs: -10.47% – 20.79%).

## 347 Discussion

348 When monkeys first learned an association between an action stimulus and an action  
349 response, individuals reinforced for a compatible rule performed significantly better than those  
350 who were reinforced for an incompatible rule. This finding is the first evidence of a

351 compatibility effect in an action SRC paradigm with nonhuman primates, contributing to  
352 existing comparative evidence in birds and dogs (Mui et al., 2008; Range et al., 2011), although  
353 it is important to highlight that this initial effect is weak (i.e., estimated CIs = 1.33% - 39.62%),  
354 and that only one monkey reached the predetermined learning criterion. The difficulty in  
355 learning a compatible action association is consistent with previous work with capuchins that  
356 has shown that while certain types of behavior matching is possible (e.g., action that requires  
357 the movement of objects), actions themselves are rarely copied (Fragaszy et al., 2011).

358         We found that the marginally superior performance of those rewarded for compatible  
359 responses in the first learning block did not persist once reward contingencies were reversed,  
360 which suggests that reinforcing certain stimulus-response associations (whether compatible or  
361 incompatible S-R associations) subsequently makes it equally difficult to learn the reversed  
362 associative rule. The comparable lack of success observed in both conditions in the second  
363 block of learning is consistent with predictions of an experience based account of imitation and  
364 similar effects observed in humans and other animals (Heyes et al., 2005; Range et al., 2011).  
365 However, as only one monkey learned an associative rule (i.e., reaching the predetermined  
366 criterion), and as we may have ended training in the second block before a compatibility effect  
367 was identifiable we conducted a second experiment to further examine the possibility of a  
368 predisposition for imitative ability. In this study we retested two monkeys from experiment one  
369 on a series of reversal learning sets to examine if a compatibility bias would be more evident  
370 in a repeated reversal design. Using the same SRC procedure used in experiment one, each  
371 monkey learned both compatible and incompatible action rules to a predetermined criterion.  
372 The small sample used in this second experiment may limit the scope of our conclusions, but  
373 if a bias to imitate is present in capuchin monkeys we may expect that following rule reversal,  
374 performance on the compatible associative rule would be overall better than on the

375 incompatible rule.

## 376 **Experiment 2: Repeated reversal learning of a stimulus-response association**

### 377 **Methods**

#### 378 **Subjects**

379 This second experiment examined repeated reversal learning of compatible and  
380 incompatible rules with two male monkeys from experiment one (Chico: 3.4 years and  
381 Carlos: 6.2 years at the beginning of experiment 2). These monkeys were selected for this  
382 experiment as they were the best learners in the initial learning blocks of their respective  
383 conditions (see first block in Table 1). These research sessions took place between October  
384 2012 and July 2013, ten months after Carlos' last session in experiment one, and four months  
385 after Chico's last session.

#### 386 **Procedure**

387 Both monkeys were tested in a similar fashion to experiment one. In the first block of  
388 learning Chico was rewarded for performing incompatible responses and Carlos was rewarded  
389 for performing compatible actions. Correct responses were rewarded with a food item and  
390 incorrect responses resulted in a three second time-out where the experimenter would turn their  
391 back to the monkey. One strategy employed by monkeys in experiment one in an effort to  
392 maximize rewards was to perform one action repeatedly (see Results of experiment 1),  
393 therefore receiving half of all rewards in each research session. To improve speed of learning  
394 and to encourage switching between actions, correctional procedures were introduced. If  
395 monkeys responded incorrectly on a trial the same trial was repeated until the monkey either  
396 performed the correct response or an incorrect response was performed a certain number of  
397 times. We expected that these training procedures would increase the likelihood that a rule will

398 be learned more quickly by forcing monkeys out of single-action biases. Furthermore, we kept  
399 these procedures consistent across conditions, so that they would not interfere in interpreting  
400 performance. Initially, a trial was repeated up to five times if an incorrect action was performed,  
401 however, five consecutive “time-outs” became an overly stringent punishment and subject  
402 participation dropped. To increase participation, incorrect responses were instead repeated 3  
403 times (this change occurred after 264 trials for Chico, and after 78 trials for Carlos). These  
404 incidences were always scored as a single incorrect trial.

405         Learning criterion in this second experiment was altered as it was felt that the initial  
406 criterion was unnecessarily strict and may have interfered with the identification of learning in  
407 some cases. In the second experiment, to qualify as having learned an associative rule, monkeys  
408 had to progress through the following stages. First, a monkey had to provide 65% or more  
409 correct responses on a test session consisting of twenty trials. Once this criterion had been met,  
410 on subsequent testing sessions monkeys were only tested on ten trial sets. To demonstrate  
411 evidence of learning, monkeys had to perform 80% or more correct responses on two  
412 consecutive sessions of ten trials (taking place at different testing sessions; i.e., a minimum of  
413 an hour between testing). This two-tier criterion was employed as we wanted to offer monkeys  
414 sufficient experience of the reward contingencies in the earlier stages of learning. However,  
415 we noticed in experiment one that monkeys would sometimes lose interest with the procedure  
416 after performing a number of consecutive correct responses (possibly due to satiation). It was  
417 predicted that reducing session length to 10 trials during later stages of learning would improve  
418 motivation to attend to the procedure and would therefore provide a better measure of learning.  
419 Furthermore, this 80% criterion was still highly unlikely to be reached by chance (i.e., 16  
420 correct responses in 20 trials is likely to occur by chance only 1.2% of the time), and so, while

421 we believe that reducing the criteria would not have made the rule easier to learn it may have  
422 made it easier to identify when a monkey had learned the rule.

423         Once this criterion was met, the associative rule being rewarded was reversed. Over the  
424 course of the experiment, Carlos reached the required criterion for the compatible rule three  
425 times and the incompatible rule twice, and Chico reached the criterion for both conditions  
426 twice. To retain comparable numbers of learning blocks for each monkey, Carlos' first four  
427 blocks of learning were analyzed. Throughout these SRC sessions we continued to begin each  
428 session with 4 color discrimination trials, to encourage participation and to ensure monkeys  
429 could perform both actions discriminately.

#### 430 **Data analyses**

431         The first response to each trial was coded as a binary response variable (correct or  
432 incorrect) – correct responses to a repeated trial were not counted. Furthermore, as monkeys  
433 reached criterion at different stages for each block of learning we examined the initial  
434 performance over the first 60 trials of each learning block. This analysis criteria serves both  
435 the function of having a comparable number of trials to compare for both Carlos and Chico  
436 (i.e., 240 trials per monkey), and a comparable number of incompatible and compatible trials  
437 (i.e., 240 trials per condition). Using a generalized linear model (GLM) with a binomial  
438 distribution and logit link function, the effect of condition (compatible/incompatible) and  
439 individual subject were examined. This analysis would determine whether an associative rule  
440 is easier to switch to after having reached a predetermined number of correct responses on the  
441 other associative rule (see above). The interaction between associative rule being rewarded  
442 (compatible versus incompatible) and subject was examined to see if performance on  
443 conditions was independent of individual monkey.

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## Results

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For descriptive data on the number of trials it took each monkey to reach the learning criteria on each learning block see Table 3. A GLM identified a significant interaction between condition and monkey (Wald test,  $\beta$  [monkey x condition] = 1.722, s.e. = 0.392,  $z = 4.390$ ,  $p < 0.001$ ; see Table 4 and Figure 2). There was no difference in performance between conditions for Chico (estimated 15.98% higher odds of success in the incompatible condition, CIs: -32.00% - 97.83%; Wald test,  $\beta$  [incompatible] = 0.148, s.e. = 0.273,  $z = 0.544$ ,  $p = 0.586$ ) and Carlos performed significantly worse on incompatible trials (odds of a correct response were 79.28% lower in the incompatible condition, CIs: 63.97% -88.08%; Wald test,  $\beta$  [incompatible] = -1.574, s.e. = 0.282,  $z = -5.576$ ,  $p < 0.001$ ).

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## Discussion

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In this second experiment, further efforts to examine imitative biases in two capuchin monkeys showed no evidence that imitative rules are intrinsically easier than counter-imitative rules over a series of learning reversals sets. As a complement to experiment one we demonstrated that both compatible and incompatible action rules can be learned by two capuchin monkeys, but that overall it is not easier to learn one associative rule over the other. One monkey did perform better when compatible trials were rewarded when compared to incompatible trials, but without further study of a larger sample, we cannot conclusively state whether this finding is driven by an imitation bias, or a bias towards a first-learned association (although, the second monkey in experiment two showed no bias towards either rule).

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## General Discussion

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In our first experiment, we report the first evidence from nonhuman primates of an imitative bias in an action stimulus response compatibility (SRC) task. In general, evidence of action imitation in monkeys is scarce, but this result complements evidence of bodily matching

468 reported in New World (Voelkl & Huber, 2000, 2007) and Old World monkeys (van de Waal  
469 & Whiten, 2012). It is worth highlighting that only one monkey reached the predetermined  
470 criterion in the initial learning block, and that in general, the difficulty that monkeys faced in  
471 transferring their previously learned color-action association skills to an action-action  
472 associative paradigm demonstrates that this imitative bias is not necessarily automatic in the  
473 sense of being reflexive and effortless. At least, the ability to match hand and mouth actions  
474 are not readily available to capuchin monkeys (also evidenced by previous research; e.g.,  
475 Frigaszy et al., 2011). Indeed, it has been argued that the ability to imitate actions may not be  
476 present in any non-human primates (Tennie, Call, & Tomasello, 2009), at least in a manner  
477 that does not require considerable training or human enculturation (e.g., Custance, Whiten, &  
478 Bard, 1995). Instead, the effect identified here may be an implicit bias that this specific  
479 procedure could tap into, and may be related to some other, non-imitative, form of social  
480 influence, such as those identified in more naturalistic contexts in primates (e.g., mimicry,  
481 response facilitation; Mancini, Ferrari, & Palagi, 2013). Given the many reinforcement trials  
482 received across these studies, the difficulty the monkeys faced in reaching the learning criteria  
483 in either condition might be puzzling. It is unclear, however, whether this problem stems from  
484 an imitative deficiency, or rather a more general problem related to the saliency of action  
485 stimuli, or short-term memory capacities for action stimuli. A more general perspective on how  
486 imitative learning fits within other domains of social cognition is largely lacking and future  
487 work with SRC methods may help understand how imitation fits within this broader context.

488         We recognize that our protocol traded ecological validity for control over stimulus  
489 presentation and ease of interpreting action responses, and so future studies may identify  
490 stronger imitative effects in more naturalistic contexts (i.e., foraging contexts). Furthermore,  
491 the use of a human demonstrator may have influenced attentional or other factors, and although

492 human demonstrators have been used in studies of imitation (Custance et al., 1995; Frigaszy  
493 et al., 2011), mirror neurons (Gallese et al., 1996; Keysers et al., 2003), and imitation  
494 recognition (Paukner, Suomi, Visalberghi, & Ferrari, 2009), the greater control facilitated by  
495 the use of an SRC task may be improved with the use of a conspecific demonstrator. In spite  
496 of how these factors were likely to have contributed to the difficulty these monkeys faced when  
497 learning this task, we demonstrated that two monkeys were able to meet a strict learning  
498 criterion in experiment two. This provided confirmation that, given enough experience,  
499 capuchins can learn to distinguish between specific human actions and respond  
500 discriminatorily. Indeed, the initial compatibility bias suggests that even in an ecologically  
501 artificial set-up, capuchin monkeys must have, to some degree, been sensitive to the  
502 correspondence between observed actions and the performance of actions using the same body-  
503 part, at least initially.

504         The controlled nature of this method, that incorporated a prolonged testing phase taking  
505 place over a number months, allows a more nuanced exploration of action matching when  
506 compared with previous efforts with primates (e.g., Voelkl & Huber, 2000; van de Waal &  
507 Whiten, 2012) where action matching is assessed from behavior that immediately follows a  
508 single observation period (for good reason, as behavior at later stages is confounded by  
509 individual learning). We believe that future work incorporating elements of our method, with  
510 a wider range of actions and stimulus-response contingencies, could be useful in determining  
511 both the action matching abilities of primates and the role of experience.

512         Our findings that an imitative bias is not present following counter-imitative experience  
513 (i.e., the second block of reinforcement trials in experiment one and experiment two), suggests  
514 that sensorimotor experience can eliminate imitative biases, complementing evidence from a  
515 range of other human studies and one finding with dogs (Catmur et al., 2008; Heyes et al.,

516 2005; Range et al., 2011). However, any conclusions concerning a lack of a strong disposition  
517 to imitate rests on null findings which must be interpreted with caution (Sainani, 2013).  
518 Furthermore, Carlos, one of the two monkeys in experiment two, did perform significantly  
519 better when rewarded for compatible responses (see Figure 2), and so it may be that an imitative  
520 bias can be maintained in certain contexts. Carlos was the only monkey in experiment one who  
521 reached the predetermined learning criterion in the initial learning block, and this initial  
522 reinforcement may have led to a persistent advantage for imitative rules across subsequent  
523 trials, conducted more than 10 months after this initial reinforcement was received. In contrast,  
524 Chico, the monkey who did not display a bias for any particular rule in experiment two, while  
525 the best performer in his initial block of incompatible learning in experiment one, did not reach  
526 the learning criterion and so was not reinforced preferentially for incompatible response to the  
527 same extent as his compatibly reinforced counterpart. This difference in reinforcement history  
528 in the first part of experiment one (see Table 1) may explain the individual differences in  
529 experiment two, but we stress that this post-hoc interpretation is highly speculative. Overall,  
530 the failure to identify strong imitative biases suggests that relationships between sensory and  
531 motor representations of actions in monkeys are malleable, at least in some contexts.

532         Given the marginal difference between conditions at the first stage of this experiment,  
533 it may not be particularly surprising that initial experience of reinforcement had the effect of  
534 minimizing an imitative bias at other stages of this study. However, this effect is notable when  
535 considering the persistence of some SRC biases in other domains. For example, one classic  
536 study of a traditional stimulus-response compatibility effect (the Simon effect) in adult humans  
537 found that compatibility effects were still present in some cases after more than 1500 trials  
538 (Fitts & Seeger, 1953), suggesting that when there is strong dimensional overlap in S-R  
539 pairings, compatibility effects persist in the face of considerable experience. Of course, there

540 may be greater overlap in the characteristics of some other S-R pairings examined with this  
541 procedure (e.g., spatial orientation; Simon & Rudell, 1967). In contrast, and as highlighted  
542 earlier, for certain actions (including the mouth action used in this study) the perceptual  
543 information available when observing one's own actions and those of another often do not  
544 correspond. Instead, in the case of some opaque actions, the associations between stimuli and  
545 action responses must be the result of either specific experience linking these (analogous to the  
546 learned associations that result in phenomena such as the Stroop effect; Stroop, 1935), or would  
547 need to be present from birth in the form of a multimodal matching system (e.g., Meltzoff &  
548 Moore, 1997). It should also be emphasized that the absence of an imitative bias following  
549 incompatible sensorimotor experience is not irreconcilable with the presence of a multimodal  
550 action matching system that exists at birth, as later learning may both inhibit or facilitate a pre-  
551 existing imitative bias, and indeed proponents of neonatal imitation accept that later learning  
552 is likely to influence imitative ability (Marshall & Meltzoff, 2014).

553         Examples of imitative learning may be rare in capuchin monkeys, but imitation  
554 recognition and the role of imitation in facilitating affiliation are also worth considering briefly.  
555 For example, capuchins and macaques recognize when the actions of human experimenters  
556 correspond to their own and seem to display affiliative behaviors towards these individuals  
557 (Paukner et al., 2009; Sclafani, Paukner, Suomi, & Ferrari, 2015). If the mechanism that links  
558 observable action to an executed action is forged through associative learning then it is possible  
559 that monkeys that have been trained to respond in counter-imitative ways may show increased  
560 interest and affiliation towards those that perform contingent non-matching actions. However,  
561 if it is discovered that imitation's role in affiliation is still present following incompatible  
562 training, then this would call into question the proposal that sensitivity to action matching is  
563 purely the result of experience. It may also be the case that the mechanisms underlying

564 imitation's role in learning and affiliation have different origins. Nonetheless, SRC tasks may  
565 in the future be a useful tool in examining the link between imitation and affiliation.

566 Overall, this study contributes to a growing understanding of action imitation in  
567 primates and the impact of experience on imitative behavior. However, this is only a first step  
568 towards understanding the types of experiences that may impact upon imitative ability in  
569 primates, and future work is necessary to understand the full extent of experiences' role not  
570 only in the elimination of imitative effects, but in the development of these effects. Further  
571 work incorporating action SRC paradigms with New and Old World primates may provide  
572 unique insight into imitative effects in nonhuman primates, and could be used to test a variety  
573 of hypotheses related to the extent and ontogeny of action matching in nonhuman animals in  
574 general.

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763 Table 1.

764 *Descriptive data from stimulus response compatibility (SRC) trials 1-500 for each monkey (320*  
 765 *trials for Kato and Sylvie) in both conditions with trial success coded as a binary variable (1*  
 766 *represents a successful response and 0 an unsuccessful one). This measure is the equivalent to*  
 767 *the proportion of correct responses in a learning block. Standard error of the mean is included*  
 768 *in brackets. See Figure 1 for a graphical representation of totals.*

Rule rewarded in 1st Reinforcement Block		Trials per learning block	Mean Trial Success (SE)	
			1st Block	2nd Block
Pedra	Incompatible	500	.506 (.022)	.522 (.022)
Figo	Incompatible	500	.500 (.022)	.478 (.022)
Chico	Incompatible	500	.572 (.022)	.444 (.022)
Kato	Incompatible	320	.500 (.028)	.478 (.028)
<b>Total</b>	<b>Incompatible</b>	<b>1820</b>	<b>.521 (.012)</b>	<b>.481 (.012)</b>
Carlos	Compatible	500	.658 (.021)	.484 (.022)
Micoe	Compatible	500	.562 (.022)	.502 (.022)
Inti	Compatible	500	.516 (.022)	.478 (.022)
Sylvie	Compatible	320	.512 (.027)	.500 (.028)
<b>Total</b>	<b>Compatible</b>	<b>1820</b>	<b>.567 (.012)</b>	<b>.490 (.012)</b>

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773 Table 2.

774 *A Generalised Linear Mixed Model with a binomial error distribution and logit link function*  
 775 *is reported below. Trial performance (correct/incorrect) was examined as the dependent*  
 776 *variable, and condition (compatible/incompatible) and order of learning (1<sup>st</sup> block/2<sup>nd</sup> block)*  
 777 *were included as fixed effects. Individual monkey was included as a random intercept in the*  
 778 *model and session number was included as a random slope.*

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<b>Random Effects</b>	<b>Variance</b>	<b>STD</b>		
Monkey (intercept)	0.0087	0.0933		
Session	0.0137	0.1169		
<b>Fixed Effects</b>	<b>Estimate</b>	<b>SE</b>	<b>z</b>	<b>p-value</b>
Intercept (Order = First, Condition=				
Compatible)	0.4499	0.1315	3.421	<0.001
Incompatible (when order = First)	-0.2589	0.1253	-2.067	0.039
Order (when condition = Compatible)	-0.5298	0.1366	-3.879	<0.001
Order * Condition	0.2981	0.1481	2.012	0.044

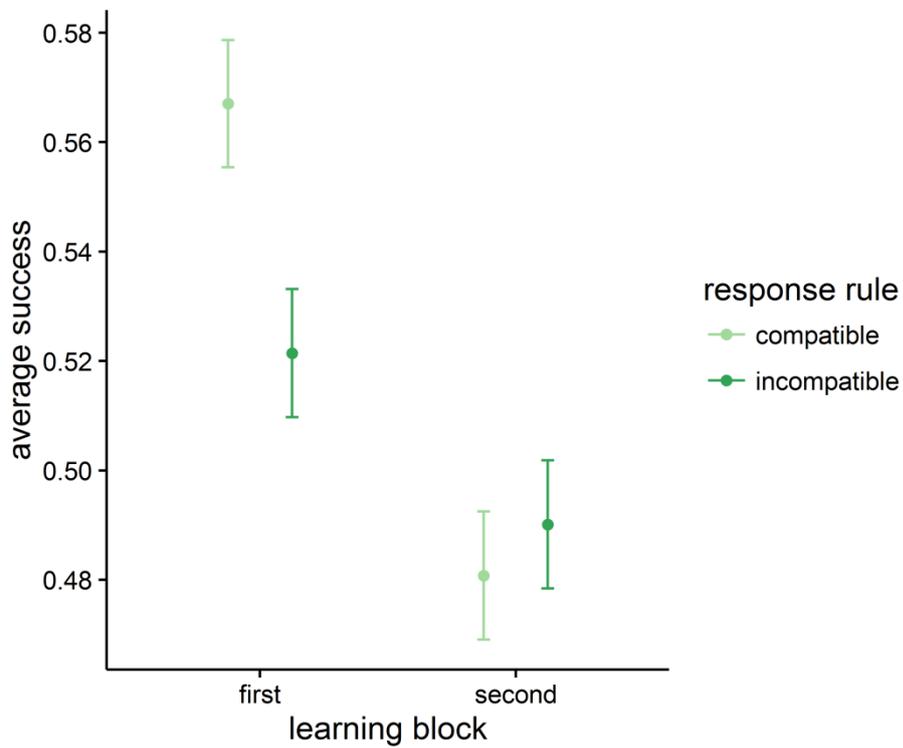
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786 *Figure 1.* Mean proportion of correct responses in the first 500 trials for compatible and  
787 incompatible conditions when associative rules are first learned and following rule reversal.

788 Error bars represent standard error of the mean.

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796 Table 3.

797 *Number of trials completed before each monkey reached learning criteria for each learning*  
 798 *block. The first letter of the rule learned is in brackets after the trial number (compatible =c;*  
 799 *incompatible =i); e.g., Carlos began learning the compatible rule while Chico began with the*  
 800 *incompatible rule.*

**Number of Trials Before Reaching Criterion**

<b>Learning Block</b>	<b>Carlos</b>	<b>Chico</b>	<b>Total</b>
1	200 (c)	204 (i)	404
2	166 (i)	267 (c)	433
3	60 (c)	551 (i)	611
4	280 (i)	541 (c)	821
5	235(c)		
<b>Total</b>	<b>941</b>	<b>1563</b>	<b>2269</b>

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809 Table 4.

810 *To examine whether condition (compatible/incompatible) and monkey (Chico/Carlos)*  
 811 *influenced trial success over the first 60 trials of each learning block, we created a*  
 812 *Generalised Linear Model with a binomial error distribution and logit link function. The full*  
 813 *model is reported below.*

<b>Fixed Effects</b>	<b>Estimate</b>	<b>SE</b>	<b>Z</b>	<b>p-value</b>
Intercept (Monkey = Carlos, Condition=				
Compatible)	0.4754	0.1878	2.532	0.011
Incompatible (when monkey = Carlos)	-1.5740	0.2823	-5.576	<0.001
Chico (when condition = compatible)	-1.2063	0.2706	-4.457	<0.001
Monkey * Condition	1.7223	0.3923	4.390	<0.001

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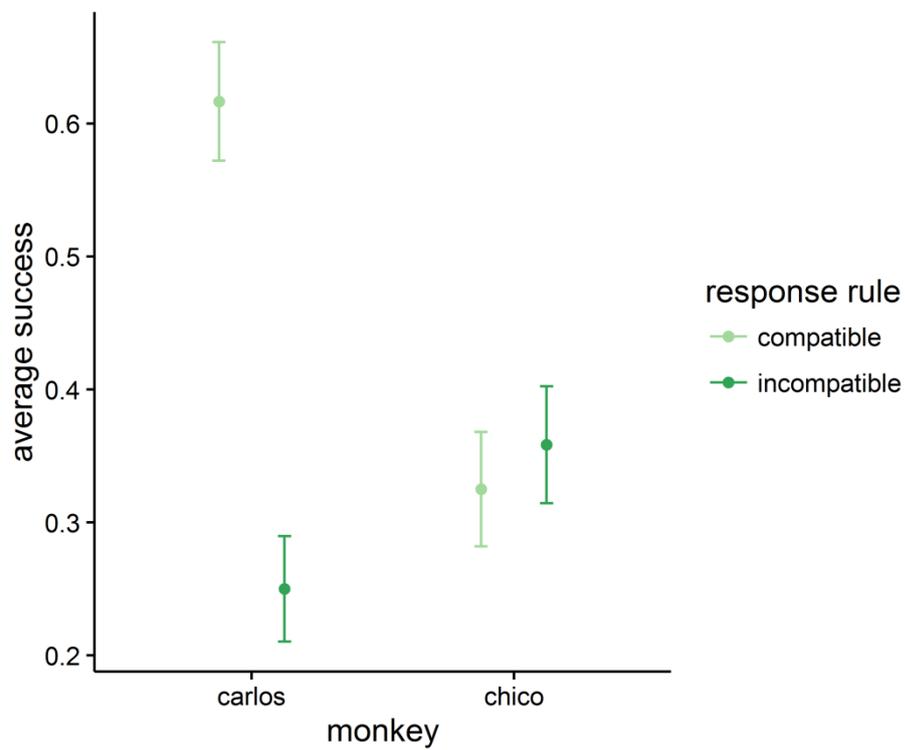
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825 *Figure 2.* Mean proportion of correct responses in experiment two over the first 60 trials of  
826 each learning block for both subjects (Carlos/Chico) differentiated by response rule. Error  
827 bars represent standard error of the means.

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