

Action-Matching Biases in Monkeys (*Sapajus spp.*) in a Stimulus–Response Compatibility Task: Evaluating Experience-Dependent Malleability

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Stimulus–response (S–R) compatibility effects occur when observing certain stimuli facilitate the performance of a related response and interfere with performing an incompatible or different response. Using stimulus–response action pairings, this phenomenon has been used to study imitation effects in humans, and here we use a similar procedure to examine imitative biases in nonhuman primates. Eight capuchin monkeys (*Sapajus spp.*) were trained to perform hand and mouth actions in a stimulus–response compatibility task. Monkeys rewarded for performing a compatible action (i.e., using their hand or mouth to perform an action after observing an experimenter use the same effector) performed significantly better than those rewarded for incompatible actions (i.e., performing an action after observing an experimenter use the other effector), suggesting an initial bias for imitative action over an incompatible S–R pairing. After a predetermined number of trials, reward contingencies were reversed; that is, monkeys initially rewarded for compatible responses were now rewarded for incompatible responses, and vice versa. In this 2nd training stage, no difference in performance was identified between monkeys rewarded for compatible or incompatible actions, suggesting any imitative biases were now absent. In a 2nd experiment, 2 monkeys learned both compatible and incompatible reward contingencies in a series of learning reversals. Overall, no difference in performance ability could be attributed to the type of rule (compatible–incompatible) being rewarded. Together, these results suggest that monkeys exhibit a weak bias toward action copying, which (in line with findings from humans) can largely be eliminated through counterimitative experience.

Keywords: stimulus–response compatibility, imitation, social learning, capuchin monkeys

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To imitate, an animal may recreate, through action, the perceived visual qualities of the act it sees performed by another. However, the visual information obtained from perceiving another animal’s actions often does not correspond to the sensory experience of observing one’s own performance of the same action;

indeed, sometimes an action is entirely opaque to the actor (e.g., when performing a facial expression). The cognitive challenge in overcoming this so-called correspondence problem (Nehaniv & Dautenhahn, 2002) might explain why researchers examining action imitation (more specifically defined as converting “visual information into matching motor acts”; Custance, Whiten, & Fredman, 1999, p. 14) in nonhuman primates have concluded that there is a qualitative difference in comparison with human abilities (Call & Tomasello, 1995; Frigaszy, Deputte, Cooper, Colbert-White, & Hémerly, 2011; Subiaul, 2016; Tennie, Call, & Tomasello, 2012; Tomasello, Davis-Dasilva, Camak, & Bard, 1987). Indeed, the question of imitative ability in animals dates to early work in the comparative tradition (Thorndike, 1911) and has continued in more recent times (Caldwell & Whiten, 2002); however, even those who have claimed nonhuman apes might possess some capacity to imitate have been more cautious when describing the abilities of monkeys (Whiten & van de Waal, 2016).

Over the last decades, researchers of social learning have documented many failed attempts to observe action imitation in monkeys (e.g., Frigaszy et al., 2011; for reviews see Frigaszy & Visalberghi, 2004; Visalberghi & Frigaszy, 2001), yet studies

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using simple, extractive foraging tasks have provided some evidence that monkeys will match the body part used by a conspecific to open containers. Voelkl and Huber (2000) found that common marmosets (*Callithrix jacchus*) were more likely to open a box with their hand after observing a conspecific use the same body part, when compared to individuals who had seen the container opened by mouth. Furthermore, a detailed frame-by-frame analysis of the video footage of these actions found that specific action characteristics measured when the monkeys opened the box with their mouth (e.g., head inclination) were significantly more alike when one monkey had watched another perform the action (in comparison to monkeys who had not observed a conspecific; Voelkl & Huber, 2007). Using a similar methodology with a larger sample of vervet monkeys (*Chlorocebus aethiops*), van de Waal and Whiten (2012) provided further evidence of body-part matching. Subjects were more likely to use their hand after observing a conspecific use that same action when opening a food-baited canister. These studies of bodily imitation in a few species of monkeys provide the extent of positive findings on motor imitation in adult monkeys, although evidence of a distinctive form of imitative behavior, which may be unrelated to the current question of imitation in adult monkeys, has also been reported in neonates (e.g., Ferrari et al., 2006).

Developmental approaches to imitation suggest certain types of experience are crucial for imitative ability to develop. For example, the associative sequence learning approach and ideomotor approach posit that imitative ability is formed through compatible sensorimotor experience; that is, the contingent experience of performing and observing the same action (Heyes, 2010; Heyes & Ray, 2000; Prinz, 1997, 2005). This sensorimotor experience could occur when infants observe their own actions or by being imitated by caregivers (Del Giudice, Manera, & Keyzers, 2009). Support for experiential accounts of imitation has been provided through the use of stimulus–response compatibility (SRC) procedures that incorporate stimulus–response (S–R) action pairs. With human adults, an action SRC task typically requires participants to perform two different actions (e.g., hand opening–closing) while simultaneously presented with a task-irrelevant image that displays either a compatible action (i.e., the action they must perform) or an incompatible action (i.e., the different action). Reaction times (RTs) are consistently quicker when the image presented corresponds with the action to be performed, whereas images of incompatible actions invoke slower responses, a phenomenon described as automatic imitation (Brass, Bekkering, & Prinz, 2001; Brass, Bekkering, Wohlschläger, & Prinz, 2000; Heyes, Bird, Johnson, & Haggard, 2005; Stürmer, Aschersleben, & Prinz, 2000). This action-specific SRC effect is similar to those found in traditional SRC procedures, where stimulus–response pairs share other overlapping characteristics (e.g., spatial location: Simon & Rudell, 1967; or semantic content: e.g., Stroop, 1935; for a review see Kornblum, Hasbroucq, & Osman, 1990) and has been proposed as a method of studying imitation, mimicry, and mirror neurons in humans (Heyes, 2011).

If some forms of imitation are modulated by sensorimotor experience, it follows that these imitation effects are malleable and should be influenced by sensorimotor training; indeed, incompatible training sessions, where participants were required to open their hand after seeing a hand close and vice versa, delivered 24 hr before an action SRC task, have been found to significantly reduce compatibility

effects in adult humans (Heyes et al., 2005). Catmur et al. (2008) used a similar method to examine activity in brain regions associated with mirror neuron activity. After participants received incompatible training (performing hand actions when presented with an image of a foot and vice versa), brain areas previously related with hand actions were active when viewing images of a foot, possibly suggesting that the neural substrates thought to facilitate imitative behavior (Gallese, Fadiga, Fogassi, & Rizzolatti, 1996; Iacoboni et al., 1999) are sensitive to experience. This evidence suggests that existing cognitive relationships between sensory-motor representations, whether innate or learned, are plastic and can adapt to varied inputs. Although nativist and empiricist approaches to imitation are not necessarily mutually exclusive, a proper understanding of the impact of experience on imitation in nonhuman primates is currently lacking, which presents a stark contrast with the efforts devoted to investigating preexisting abilities.

With human participants, SRC effects identified using action S–R pairings are examined using RT measurements. These effects occur when participants (required to perform specific responses) are unintentionally and automatically influenced by action stimuli in accordance with the compatibility state of the S–R pairing (Brass et al., 2000; Catmur & Heyes, 2011; Stürmer et al., 2000). Compatible S–R pairings therefore typically facilitate performance (fast RTs), whereas incompatible pairings tend to produce interference (slower RTs). Studies that have examined this SRC effect in nonhuman animals have followed a different approach (Mui, Haselgrove, Pearce, & Heyes, 2008; Range, Huber, & Heyes, 2011). Instead of examining RT response, subjects are trained to respond with two different actions discriminatively to two action stimuli, and associations between stimuli and responses are learned by trial and error. Subsequently, the learning success of subjects reinforced for compatible S–R pairings (i.e., rewarded for performing the same action they see) is compared with the success of animals reinforced for incompatible S–R pairings (i.e., rewarded for performing an action different from the one they see). If compatible pairings are learned more quickly than incompatible pairings, it is inferred that the perceptual qualities of the action stimuli aids in the performance of the same action over a different action, indicative of an imitative ability or bias. Given the training procedure, it is less clear that the compatibility effects can be said to be “automatic,” and so the term *automatic imitation* may be less suited to these findings (although to date, the comparative literature has been described using this terminology; i.e., Mui et al., 2008; Range et al., 2011).

Using this comparative methodology, budgerigars (*Melopsittacus undulatus*) rewarded for imitating a conspecific that performed a foot versus a beak action have been found to learn the associative rule more quickly than have subjects rewarded for performing an opposite action (Mui et al., 2008). Similarly, domestic dogs (*Canis lupus familiaris*) rewarded for opening a door with the same body part as their owner (either hand–paw or mouth), learned this rule faster than those rewarded for using the opposite body part (Range et al., 2011). Furthermore, in the Range et al. (2011) study of imitative biases in dogs, it was found that once the animals were reinforced for incompatible rules, their subsequent performance on compatible actions was poorer when compared to dogs that had not experienced incompatible training. The authors concluded that this suggests that previous incompatible experience carried over into the subsequent condition where only imitation was rewarded, which is consistent with experiential accounts of imitative ability.

The use of these learning procedures provides a method of assessing whether S–R associations relevant to bodily imitation are facilitated by compatibility effects, thus providing a means by which underlying biases can potentially be revealed.

In the current study, our aims were twofold. First, using an SRC paradigm, we examined whether capuchin monkeys (*Sapajus spp.*) would find compatible S–R action pairings (i.e., when hand actions were rewarded following presentation of a hand-action stimulus and where mouth actions were rewarded following presentation of a mouth-action stimulus) easier to learn in comparison to incompatible pairings (i.e., when hand actions were rewarded following presentation of a mouth-action stimulus and vice versa). Capuchin monkeys are New World primates that interest researchers of social learning because of their high brain-to-body-mass ratio (see Frigaszy, Visalberghi, & Fedigan, 2004), socially tolerant nature (Frigaszy, Feuerstein, & Mitra, 1997), tool use capacities (Visalberghi, 1993), and evidence of socially learned traditions in wild populations (Perry, 2011). Capuchins have been studied extensively to examine their social learning abilities (Addessi & Visalberghi, 2001; Dindo, Thierry, & Whiten, 2008; Dindo, Whiten, & de Waal, 2009; Frigaszy et al., 2011), yet no clear evidence of action imitation has been identified in this species (e.g., Frigaszy et al., 2011). However, though previous studies have suggested capuchin monkeys learn primarily from nonimitative forms of social learning (Craat, Hardy, & Frigaszy, 2010; Frigaszy et al., 2011; Galloway, Addessi, Frigaszy, & Visalberghi, 2005), the methodology employed here permitted investigation of subtler imitative biases. Second, if an imitative bias was identified, we hoped to examine if this bias was resistant to counter-imitative training.

In Experiment 1 we address both of these aims. Capuchin monkeys were rewarded for performing actions with their hand and mouth discriminatively upon observing an experimenter perform hand and mouth actions. Half of the monkeys were reinforced for performing the same action they observed the experimenter perform (i.e., performing hand actions to hand stimuli; mouth actions to mouth stimuli), and the other monkeys were rewarded for performing the alternative action (i.e., performing hand actions to mouth stimuli; mouth actions to hand stimuli). We predicted that if capuchin monkeys enter into this procedure with some bias to imitate specific motor actions, they would perform better when rewarded for the compatible rule. Following this first set of training activities, the reinforcement of S–R contingencies was reversed; that is, monkeys that were initially rewarded for compatible responses were rewarded for performing incompatible responses, and vice versa. If capuchin monkeys possess a strong disposition to imitate (whether learned or innate), it might be expected that during this reversal-learning stage those learners switching from an incompatible rule to a compatible rule would perform better than would individuals that experience the alternate reversal.

Experiment 1: Two-Action Stimulus–Response Compatibility Task

Method

Subjects and research site. Eight capuchin monkeys (*Sapajus spp.*) were tested in Experiment 1 (six male; mean age at the beginning of the study was 3.9 years, $SD = 2.0$; range = 1.4–7.5). All monkeys were housed in one of two mixed-species groups with squirrel monkeys (*Saimiri sciureus*) at the Living Links to Human

Evolution Research Centre at Edinburgh Zoo in Scotland. The monkeys were never food- or water-deprived, and all rewards offered during research sessions were supplementary to their diet. Before this experiment took place, these capuchins had been studied on a range of cognitive tasks (e.g., Morton, Lee, & Buchanan-Smith, 2013); however, no previous study had examined action imitation. Ethical approval was granted by the University of Stirling Psychology Ethics Committee, and all research took place between February 2011 and June 2012.

Materials. Eight research cubicles arranged in a connected 2×4 matrix act as a corridor between the monkeys' indoor and outdoor enclosures (each cubicle measures 49.5 cm \times 52.1 cm \times 51.4 cm). Partitioning slides inserted between cubicles allow monkeys to be separated from their groupmates for research purposes. The cubicle window (i.e., the Perspex screen orientated toward the experimenter) included a small opening in its center, allowing juice to be delivered to the capuchins through a mouthpiece connected to a rubber tube and syringe. On the bottom left side of the cubicle window was a hole (3.5-cm diameter) through which food rewards were offered. To shape two disparate actions, we used a modified table tennis paddle (see the online supplemental materials, Video 1.). Alternate sides were colored black and white to facilitate color-discrimination training. A second target was used during the stimulus–response compatibility (SRC) trials that differed in shape and color (see the online supplemental materials, Video 2). Sessions were recorded on a Sony Mini DV Digital Video Camera.

Shaping behaviors. For monkeys to take part in SRC trials, two actions employing disparate body parts were trained: touching the cubicle window with (a) their hand and (b) their mouth. These specific actions were used because they were considered similar to those used in previous comparative work (Mui et al., 2008; Range et al., 2011) but were also trainable through reinforcement. These actions are not incompatible in the sense of their performance being mutually exclusive (e.g., opening vs. closing a hand), but the use of disparate body parts has been common practice when studying imitation in primates (e.g., Voelkl & Huber, 2000) as well as stimulus–response compatibility effects in humans and other animals (Catmur & Heyes, 2011; Gillmeister, Catmur, Liepelt, Brass, & Heyes, 2008; Mui et al., 2008; Range et al., 2011). The training of both actions took place concurrently through positive reinforcement of successive approximations of each action.

To train each individual to touch the cubicle window with its mouth, we delivered diluted fruit juice (one part juice to two parts water) from a syringe to the mouthpiece on the inside of the cubicle. Capuchins learned to bring their mouths to the screen to receive the juice reward. Next, the experimenter (EO) presented the training target ~ 5 cm in front of the window before the juice was delivered. Once capuchins learned to bring their mouths to the window before the juice was delivered, the juice reward was replaced with a food reward. In some instances the monkeys would use their hands to balance themselves against the Perspex screen when performing the mouth action, but this action was still interpreted as a mouth action, because the goal was to place their mouth against the screen. To train a distinct hand action, we presented the training target to the small hole where food rewards were offered. The target was removed once touched by the subject's hand, and a food reward was offered. Gradually, the target was moved further from the hole, and the subject, unable to touch the target

directly, was rewarded for touching the window with one or two hands. A monkey was never rewarded for a hand action if its mouth was also presented to the screen. At this point the learned association between stimulus and action was spatial in nature (the mouth action cued by the target presented near the center of the window; the hand action cued by the target presented nearer the left of the window).

Color-discrimination learning. Once actions had been shaped and were performed reliably to spatial cues, the target was presented only in the center of the window, and to be rewarded, the capuchin was required to learn a color-association rule (see the online supplemental materials, Video 1). The same target (see the online supplemental materials, Video 1) was used to cue both actions, but a different colored side was used in each case (i.e., for four monkeys the black side was always presented when training hand actions and the white side was always presented during the training of mouth actions; the opposite color–action pairing was reinforced for the other four monkeys). Only correct responses were rewarded, that is, performing an action that corresponded to a specific color, and if an incorrect response was performed, the experimenter turned his back on the monkey for approximately 3 s, a form of negative punishment, removing the opportunity to receive further rewards for a short time period. Once an individual had performed over 85% correct responses on three consecutive research sessions (20 trials per session), the monkey began the SRC trials.

Stimulus–response compatibility (SRC) trials. Upon completion of the color-discrimination trials, individuals were transferred into one of two groups: a compatible condition or an incompatible condition. During these SRC trials, the color stimulus was switched for an action stimulus (i.e., instead of seeing a black target or a white target on a given trial, the monkey would see the experimenter touch a target with either his hand or his mouth). Based on performance in the initial color-discrimination stage, groups were counterbalanced to include equal numbers of quick discrimination learners (mean number of research sessions before reaching criterion on the color-discrimination task was 45.75 for subjects in the compatible condition and 45 for subjects in the incompatible condition). On each research session, we attempted to complete 20 SRC trials with each monkey; however, monkeys could end the research session by demonstrating cues to leave, and so some sessions included fewer trials. During an SRC trial, a second target (see the online supplemental materials, Video 2) was held in front of the experimenter with his left hand and touched with either (a) his right hand or (b) his mouth. The target was then moved to ~5 cm in front of the window. The number of hand and mouth actions performed by the experimenter was kept equal throughout these sessions, that is, 10 mouth and 10 hand actions, and the order of hand and mouth stimuli was pseudorandomized (the maximum number of repeats was one; e.g., the stimuli performed in half of an SRC session might proceed as follows: Hand[H]-Mouth[M]-H-H-M-H-M-M-H-M). Individuals in the compatible condition were rewarded for performing actions using the same body part as the experimenter; that is, if the experimenter touched the target with his hand, the monkey was rewarded for performing an action with its hand; and if the target was touched by the experimenter's mouth, the monkey was rewarded for using its mouth). Individuals in the incompatible condition were rewarded for using the opposite actions; if the experimenter touched the target with

his hand, the monkey was rewarded for performing an action with its mouth, and vice versa.

If an action response was ambiguous (i.e., hand placed against the window on its own and then quickly replaced with a mouth response) the trial was not coded correct or incorrect, instead, the target was removed by the experimenter and the trial was repeated. A correct response was rewarded with a food item, and an incorrect response resulted in the experimenter turning his back on the monkey for approximately 3 s. Actions were judged to be correct or incorrect by the experimenter during the research session, but all sessions were video-recorded for subsequent reliability coding. A random sample of 550 action responses (6%) were extracted from video recordings, and information about the action performed by the experimenter (i.e., action stimulus presented) and trial outcome (i.e., whether the monkey was rewarded) was removed. These actions were recoded by the same experimenter who had conducted the experiment, and although this individual was not naïve to the hypotheses, the removal of contextual cues made it impossible to know whether an action performed by a monkey was in response to the same action or a different action. Agreement between the experimenter's decision within the research session and without contextual information was high ($\kappa = .97, p < .001$). Once a predetermined learning criterion was reached ($\geq 85\%$ correct responses in three consecutive 20-trial sessions), the reward contingency was to be reversed. However, only one monkey had reached this criterion before 900 trials, and due to time constraints, monkeys were switched to the other reinforcement condition regardless of progress after 900 trials, and a further 500 trials were completed by each monkey. Two monkeys were tested on fewer trials in each condition to examine performance on both associative rules without the potential confounding effects of overtraining (320 trials in each condition). Because monkeys were free to leave in the middle of sessions and the goal of each session was to test monkeys with 20 trials, monkeys completed on average 10.4 trials more than the established cutoff.

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

Data analysis. The monkeys' success on each trial was recorded as a binary response variable (either correct or incorrect). This binary variable was used as the outcome variable in a generalized linear mixed model (GLMM) with a binomial distribution and logit link function to test specific hypotheses concerning imitative biases in the SRC paradigm. Because each monkey received multiple trials in each condition, the monkey being tested was included as a random intercept in the GLMMs. Furthermore, session number (i.e., consecutive blocks of 20 trials) was included as a random slope in the models. To test hypotheses concerning the persistence of an imitative effect, we created a model with an interaction included for condition and order of learning. To describe the contribution of predictor variables to trial success, we calculated odds ratios by back-transforming the log odds ratios. All

statistical tests were conducted with the R statistics program (R Core Team, 2014) in the RStudio environment (RStudio Team, 2014). Models were developed using the lme4 package (Bates, Mächler, Bolker, & Walker, 2015), and graphics were created using the ggplot2 package (Wickham, 2009). Monkeys completed up to 900 trials in Block 1 of learning, but for two reasons only the first 500 trials for each monkey were examined (320 in the case of two monkeys). First, one monkey's response rule was switched after 500 trials, so a comparison between groups was balanced at this point (see the online supplemental materials, Figures 1 and 2, for all performance data summarized for each monkey; areas highlighted in light gray were analyzed). Also, to examine any preexisting bias in automatic imitative ability, it is more appropriate to examine earlier performances.

Results

Overall, monkeys were biased toward mouth actions, performing this action in 54.54% of all analyzed trials. Every monkey developed an effector preference at some stage of the experiment; that is, the same action was used consistently across a session. For example, when looking at diversity of action performance, we found that across all monkeys and testing sessions, on average, 90.9% of responses within a 20-trial session consisted of one type of action (although this bias could alternate across sessions; e.g., a monkey that performed mainly hand actions in one session might change to mouth responses in the following session). Because trial success in this context was unlikely to be related to a learned association between a specific stimulus and response and because overall success above a 50% chance level required a diversity of actions, effector was not examined as a predictor of success.

Descriptive data on overall performance for each monkey can be found in Table 1 (also see the online supplemental materials, Figures 1 and 2, for all performance data plotted chronologically by session). A GLMM found a significant interaction between the rule being rewarded (compatible–incompatible) and the order in which the rule was learned (Condition \times Order interaction, Wald test, $\beta = .298$, $SE = .148$, $z = 2.012$, $p = .044$; see Table 2 for the

full model; see Figure 1). In Block 1 of discrimination learning, the chance of success was significantly lower when learning an incompatible rule (an estimated 22.81% lower odds of being correct; 95% confidence interval [CI: 1.33, 39.62]; Wald test, $\beta = -.259$, $SE = .125$, $z = -2.067$, $p = .039$; see Figure 1 when order = first), but in Block 2 of learning (i.e., after response rules were switched), the type of associative rule being rewarded did not influence chance of success (Wald test, $\beta = .039$, $SE = .076$, $z = .512$, $p = .608$; see Figure 1 when order = second; estimated 3.99% greater odds of success on an incompatible trial, 95% CI [-10.47, 20.79]).

Discussion

When monkeys first learned an association between an action stimulus and an action response, individuals reinforced for a compatible rule performed significantly better than those who were reinforced for an incompatible rule. This finding is the first evidence of a compatibility effect in an action SRC paradigm with nonhuman primates, contributing to existing comparative evidence in birds and dogs (Mui et al., 2008; Range et al., 2011), although it is important to highlight that this initial effect is weak (i.e., estimated 95% CI [1.33, 39.62]) and that only one monkey reached the predetermined learning criterion. The difficulty in learning a compatible action association is consistent with findings in previous work with capuchins, which has shown that although certain types of behavior matching is possible (e.g., action that requires the movement of objects), actions themselves are rarely copied (Fragaszy et al., 2011).

We found that the marginally superior performance of those rewarded for compatible responses in the first learning block did not persist once reward contingencies were reversed, which suggests that reinforcing certain stimulus–response associations (whether compatible or incompatible S–R associations) subsequently makes it equally difficult to learn the reversed associative rule. The comparable lack of success observed in both conditions in Block 2 of learning is consistent with predictions of an experience-based account of imitation and similar effects observed

Table 1
Mean Success of Each Capuchin Monkey on the Stimulus-Response Compatibility Task in Experiment 1

Rule rewarded in learning block 1 and subject	Trials per learning block	Mean trial success (<i>SE</i>)	
		Block 1	Block 2
Incompatible			
Pedra	500	.506 (.022)	.522 (.022)
Figo	500	.500 (.022)	.478 (.022)
Chico	500	.572 (.022)	.444 (.022)
Kato	320	.500 (.028)	.478 (.028)
Total	1,820	.521 (.012)	.481 (.012)
Compatible			
Carlos	500	.658 (.021)	.484 (.022)
Micoe	500	.562 (.022)	.502 (.022)
Inti	500	.516 (.022)	.478 (.022)
Sylvie	320	.512 (.027)	.500 (.028)
Total	1,820	.567 (.012)	.490 (.012)

Note. Trial success was coded as a binary variable (1 = successful response; 0 = unsuccessful response). Mean trial success is equivalent to the proportion of correct responses in a learning block. In learning block 2, monkeys were rewarded for the opposite contingency to block 1.

Table 2
Results of the Statistical Model Used in Experiment 1

Variable	Variance	SD	<i>z</i>	<i>p</i>
Random effects				
Monkey (intercept)	.0087	.0933		
Session	.0137	.1169		
	Estimate	SE		
Fixed effects				
Intercept (order = first, condition = compatible)	.4499	.1315	3.421	<.001
Incompatible (when order = first)	-.2589	.1253	-2.067	.039
Order (when condition = compatible)	-.5298	.1366	-3.879	<.001
Order × Condition	.2981	.1481	2.012	.044

Note. In this model, Trial performance (correct–incorrect) was examined as the dependent variable, and condition (compatible–incompatible) and order of learning (Block 1–Block 2) were included as fixed effects. Individual monkey was included as a random intercept in the model, and session number was included as a random slope.

in humans and other animals (Heyes et al., 2005; Range et al., 2011). However, because only one monkey learned an associative rule (i.e., reaching the predetermined criterion), and because we may have ended training in Block 2 before a compatibility effect was identifiable, we conducted a second experiment to further examine the possibility of a predisposition for imitative ability. In this study, we retested two monkeys from Experiment 1 on a series of reversal learning sets to examine whether a compatibility bias would be more evident in a repeated reversal design. Using the same SRC procedure used in Experiment 1, we had each monkey learn both compatible and incompatible action rules to a predetermined criterion. The small sample used in Experiment 2 may limit the scope of our conclusions, but if a bias to imitate is present in capuchin monkeys, one may expect that following rule reversal,

performance on the compatible associative rule would be overall better than on the incompatible rule.

Experiment 2: Repeated Reversal Learning of a Stimulus–Response Association

Method

Subjects. Experiment 2 examined repeated reversal learning of compatible and incompatible rules with two male monkeys from Experiment 1: Chico (3.4 years old at the beginning of Experiment 2) and Carlos (6.2 years). These monkeys were selected for this experiment because they were the best learners in the initial learning blocks of their respective conditions (see Block 1 in Table 1). These research sessions took place between October 2012 and July 2013, which was 10 months after Carlos's last session in Experiment 1, and 4 months after Chico's last session.

Procedure. Both monkeys were tested in a fashion similar to that in Experiment 1. In Block 1 of learning, Chico was rewarded for performing incompatible responses and Carlos was rewarded for performing compatible actions. Correct responses were rewarded with a food item, and incorrect responses resulted in a 3-s time-out where the experimenter would turn his back on the monkey. One strategy employed by monkeys in Experiment 1 in an effort to maximize rewards was to perform one action repeatedly (see the Results section of Experiment 1), therefore receiving half of all rewards in each research session. To improve speed of learning and to encourage switching between actions, we introduced correctional procedures. If monkeys responded incorrectly on a trial, the same trial was repeated until the monkey either performed the correct response or an incorrect response was performed a certain number of times. We expected that these training procedures would increase the likelihood that a rule would be learned more quickly by forcing monkeys out of single-action biases. Furthermore, we kept these procedures consistent across conditions, so that they would not interfere in interpreting performance. Initially, a trial was repeated up to five times if an incorrect action was performed; however, five consecutive

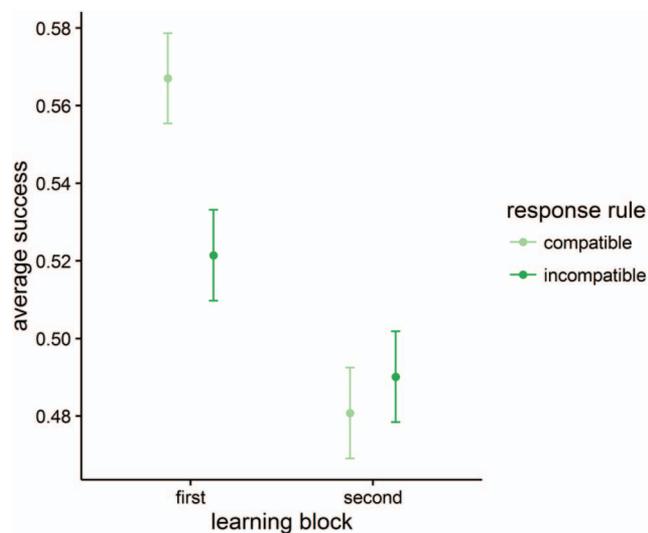


Figure 1. Mean proportion of correct responses in the first 500 trials of Experiment 1 for compatible and incompatible conditions when response rules are first learned (first learning block) and following rule reversal (second learning block). Error bars represent standard error of the mean. See the online article for the color version of this figure.

time-outs became an overly stringent punishment and subject participation dropped. To increase participation, we instead repeated incorrect responses three times (this change occurred after 264 trials for Chico and after 78 trials for Carlos). These trials with corrections were always scored as a single incorrect trial.

The learning criterion in Experiment 2 was altered because it was felt that the initial criterion was unnecessarily strict and may have interfered with the identification of learning in some cases. In Experiment 2, to qualify as having learned an associative rule, monkeys had to progress through the following stages. First, a monkey had to provide 65% or more correct responses on a test session consisting of 20 trials. Once this criterion had been met, on subsequent testing sessions monkeys were tested on only 10 trial sets. To demonstrate evidence of learning, monkeys had to perform 80% or more correct responses on two consecutive sessions of 10 trials (taking place at different testing sessions; i.e., a minimum of an hour between testing). This two-tier criterion was employed because we wanted to offer monkeys sufficient experience of the reward contingencies in the earlier stages of learning. However, we noticed in Experiment 1 that monkeys would sometimes lose interest in the procedure after performing a number of consecutive correct responses (possibly due to satiation). It was predicted that reducing session length to 10 trials during later stages of learning would improve motivation to attend to the procedure and would therefore provide a better measure of learning. Furthermore, this 80% criterion was still highly unlikely to be reached by chance (i.e., 16 correct responses in 20 trials is likely to occur by chance only 1.2% of the time), and so we believe that although reducing the criterion would not have made the rule easier to learn, it may have made it easier to identify when a monkey had learned the rule.

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

Data analyses. The first response to each trial was coded as a binary response variable (correct or incorrect), and correct responses to a repeated trial were not counted. Furthermore, because the monkeys reached criterion at different stages for each block of learning, we examined the initial performance over the first 60 trials of each learning block. This analysis criterion serves the function of having both a comparable number of trials to compare for both Carlos and Chico (i.e., 240 trials per monkey) and a comparable number of incompatible and compatible trials (i.e., 240 trials per condition). Using a generalized linear model (GLM) with a binomial distribution and logit link function, we examined the effect of condition (compatible–incompatible) and individual subject. This analysis would determine whether an associative rule was easier to switch to after having reached a predetermined number of correct responses on the other associative rule. The interaction between associative rule being rewarded (compatible

vs. incompatible) and subject was examined to see whether performance on conditions was independent of individual monkey.

Results

For descriptive data on the number of trials it took each monkey to reach the learning criterion on each learning block, see Table 3. A GLM identified a significant Condition \times Monkey interaction (Wald test, $\beta = 1.722$, $SE = .392$, $z = 4.390$, $p < .001$; 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, 95% CI $[-32.00, 97.83]$; Wald test, $\beta = .148$, $SE = .273$, $z = .544$, $p = .586$), and Carlos performed significantly worse on incompatible trials (odds of a correct response were 79.28% lower in the incompatible condition, 95% CI $[63.97, 88.08]$; Wald test, $\beta = -1.574$, $SE = .282$, $z = -5.576$, $p < .001$).

Discussion

In Experiment 2, further efforts to examine imitative biases in two capuchin monkeys found no evidence that imitative rules are intrinsically easier than counterimitative rules over a series of learning reversal sets. We demonstrated that, as a complement to Experiment 1, 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 toward a first-learned association (although, the second monkey in Experiment 2 showed no bias toward either rule).

General Discussion

In Experiment 1, we reported 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 has been scarce, but this result complements evidence of bodily matching reported in New World (Voelkl & Huber, 2000, 2007) and Old World (van de Waal & Whiten, 2012) monkeys. It

Table 3
Trials Completed Before Each Monkey Reached the Learning Criterion in Each Learning Block in Experiment 2

Learning block	No. trials before reaching criterion		
	Carlos	Chico	Total
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)		
Total	941	1563	2269

Note. The first letter of the rule learned appears in parentheses after the trial number (c = compatible; i = incompatible). For example, Carlos began with learning the compatible rule, whereas Chico began with learning the incompatible rule.

Table 4
Results of the Statistical Model Used in Experiment 2

Fixed effects	Estimate	SE	z	p
Intercept (monkey = Carlos, condition = compatible)	.4754	.1878	2.532	.011
Incompatible (when monkey = Carlos)	−1.5740	.2823	−5.576	<.001
Chico (when condition = compatible)	−1.2063	.2706	−4.457	<.001
Monkey × Condition	1.7223	.3923	4.390	<.001

Note. Trial performance (correct–incorrect) was examined as the dependent variable, and condition (compatible–incompatible) and monkey (Carlos–Chico) were included as fixed effects. Test period was the first 60 trials of each learning block.

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

We recognize that our protocol traded ecological validity for control over stimulus presentation and ease of interpreting action responses, and so future studies may identify stronger imitative effects in more naturalistic contexts (i.e., foraging contexts). Furthermore, the use of a human demonstrator may have influenced attentional or other factors, and although human demonstrators have been used in studies of imitation (Custance et al., 1995; Frigaszy et al., 2011), mirror neurons (Gallese et al., 1996; Keysers et al., 2003), and imitation recognition (Paukner, Suomi, Visalberghi, & Ferrari, 2009), the greater control facilitated by the use of an SRC task may be improved with the use of a conspecific demonstrator. Despite how these factors were likely to have contributed to the difficulty these monkeys faced when learning this task, we demonstrated that two monkeys were able to meet a strict learning criterion in Experiment 2. This provided confirmation that, given enough experience, capuchins can learn to distinguish between specific human actions and respond discriminatively. Indeed, the initial compatibility bias suggests that even in an ecologically artificial setup, these capuchin monkeys must have, to

some degree, been sensitive to the correspondence between observed actions and the performance of actions using the same body part, at least initially.

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

Our findings that an imitative bias is not present following counterimitative experience (i.e., Block 2 of reinforcement trials in Experiment 1 and Experiment 2), suggests that sensorimotor experience can eliminate imitative biases, complementing evidence from a range of other human studies (e.g., Catmur et al., 2008;

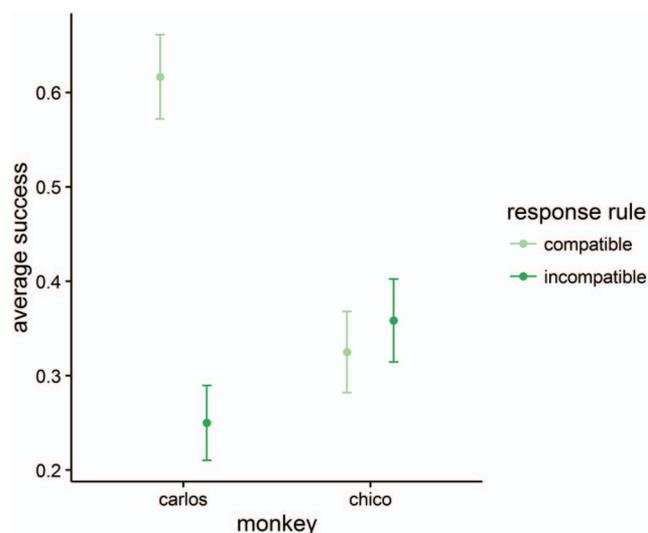


Figure 2. Mean proportion of correct responses in Experiment 2 over the first 60 trials of each learning block for both subjects (Carlos and Chico), differentiated by response rule (compatible and incompatible). Error bars represent standard error of the means. See the online article for the color version of this figure.

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

Given the marginal difference between conditions at the first stage of this experiment, it may not be particularly surprising that initial experience of reinforcement had the effect of minimizing an imitative bias at other stages of this study. However, this effect is notable when considering the persistence of some SRC biases in other domains. For example, one classic study of a traditional stimulus–response compatibility effect (the Simon effect) in adult humans found that compatibility effects were still present in some cases after more than 1,500 trials (Fitts & Seeger, 1953), suggesting that when there is strong dimensional overlap in S–R pairings, compatibility effects persist in the face of considerable experience. Of course, there may be greater overlap in the characteristics of some other S–R pairings examined with this procedure (e.g., spatial orientation; Simon & Rudell, 1967). In contrast, and as highlighted earlier, for certain actions (including the mouth action used in this study) the perceptual information available when observing one’s own actions and those of another often do not correspond. Instead, in the case of some opaque actions, the associations between stimuli and action responses must either be the result of specific experience linking these (analogous to the learned associations that result in phenomena such as the Stroop effect; Stroop, 1935) or would need to be present from birth in the form of a multimodal matching system (e.g., Meltzoff & Moore, 1997). It should also be emphasized that the absence of an imitative bias following incompatible sensorimotor experience is not irreconcilable with the presence of a multimodal action matching system that exists at birth, because later learning may both inhibit and facilitate a preexisting imitative bias, and indeed proponents of neonatal imitation accept that later learning is likely to influence imitative ability (Marshall & Meltzoff, 2014).

Examples of imitative learning may be rare in capuchin monkeys, but imitation recognition and the role of imitation in facilitating affiliation are also worth considering briefly. For example, capuchins and macaques recognize when the actions of human experimenters correspond to their own and seem to display affili-

ative behaviors toward these individuals (Paukner et al., 2009; Sclafani, Paukner, Suomi, & Ferrari, 2015). If the mechanism that links observable action to an executed action is forged through associative learning, then it is possible that monkeys that have been trained to respond in counterimitative ways may show increased interest and affiliation toward those that perform contingent nonmatching actions. However, if it is discovered that imitation’s role in affiliation is still present following incompatible training, then this would call into question the proposal that sensitivity to action matching is purely the result of experience. It may also be the case that the mechanisms underlying imitation’s role in learning and affiliation have different origins. Nonetheless, in the future SRC tasks may be a useful tool in examining the link between imitation and affiliation.

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

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Call for Nominations

The Publications and Communications (P&C) Board of the American Psychological Association has opened nominations for the editorships of the *Journal of Experimental Psychology: Animal Learning and Cognition*, *Neuropsychology*, and *Psychological Methods* for the years 2020 to 2025. Ralph R. Miller, PhD, Gregory G. Brown, PhD, and Lisa L. Harlow, PhD, respectively, are the incumbent editors.

Candidates should be members of APA and should be available to start receiving manuscripts in early 2019 to prepare for issues published in 2020. Please note that the P&C Board encourages participation by members of underrepresented groups in the publication process and would particularly welcome such nominees. Self-nominations are also encouraged.

Search chairs have been appointed as follows:

- *Journal of Experimental Psychology: Animal Learning and Cognition*, Chair: Stevan E. Hobfoll, PhD
- *Neuropsychology*, Chair: Stephen M. Rao, PhD
- *Psychological Methods*, Chair: Mark B. Sobell, PhD

Candidates should be nominated by accessing APA's EditorQuest site on the Web. Using your browser, go to <https://editorquest.apa.org>. On the Home menu on the left, find “Guests/Supporters.” Next, click on the link “Submit a Nomination,” enter your nominee's information, and click “Submit.”

Prepared statements of one page or less in support of a nominee can also be submitted by e-mail to Sarah Wiederkehr, P&C Board Editor Search Liaison, at swiederkehr@apa.org.

Deadline for accepting nominations is Monday, January 8, 2018, after which phase one vetting will begin.