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Understanding Imitation in *Papio papio*: The Role of Experience and the Presence of a Conspecific Demonstrator

Anthony Formaux,[a,b,c] Eoin O'Sullivan,[d] Joël Fagot,[a,b,c]
Nicolas Claidière[a,b,c]

[a]*Laboratoire de Psychologie Cognitive (LPC), Aix Marseille Univ, CNRS*
[b]*Laboratoire de Psychologie Cognitive (LPC), CNRS*
[c]*Station de Primatologie-Celphedia, CNRS*
[d]*School of Psychology and Neuroscience, The University of St. Andrews*

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Abstract

What factors affect imitation performance? Varying theories of imitation stress the role of experience, but few studies have explicitly tested its role in imitative learning in non-human primates. We tested several predictions regarding the role of experience, conspecific presence, and action compatibility using a stimulus–response compatibility protocol. Nineteen baboons separated into two experimental groups learned to respond by targeting on a touch screen the same stimulus as their neighbor (compatible) or the opposite stimulus (incompatible). They first performed the task with a conspecific demonstrator (social phase) and then a computer demonstrator (ghost phase). After reaching a predetermined success threshold, they were then tested in an opposite compatibility condition (i.e., reversal learning conditions). Seven baboons performed at least two reversals during the social phase, and we found no significant difference between the compatible and incompatible conditions, although we noticed slightly faster response times (RTs) in the compatible condition that disappeared after the first reversal. During the ghost phase, monkeys showed difficulties in learning the incompatible condition, and the compatible condition RTs tended to be slower than during the social phase. Together, these results suggest that (a) there is no strong movement compatibility effect in our task and that (b) the presence of a demonstrator plays a role in eliciting correct responses but is not essential as has been previously shown in human studies.

Keywords: Automatic imitation; Social learning; Stimulus–response compatibility; Mirror neuron; Guinea baboon; Ghost demonstrator

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Correspondence should be sent to Nicolas Claidière, Laboratoire de Psychologie Cognitive, UMR7290, Université Aix-Marseille/CNRS, 13331 Marseille, France. E-mail: nicolas.claidiere@cnrs.fr

1. Introduction

Imitation has been defined in various ways in the comparative and human literature (for a review, see O'Sullivan & Caldwell, 2018), with researchers emphasizing to various extents the importance of the novelty of actions copied or an understanding of goals or intentions (Byrne, 2002; Subiaul, 2010). However, in purely behavioral terms, imitation has been described simply as the matching of topographical features of another's behavior (O'Sullivan & Caldwell, 2018). To imitate someone's movements (e.g., when someone sticks out their tongue), one must match the movements being observed to one's own body movements, often having little or no visual access to one's own actions. This is commonly referred to as the "correspondence problem" (Nehaniv & Dautenhahn, 2002), and a number of theories have been proposed to explain how humans and animals might solve this "problem." Multi-level theories of imitation propose the capacity to imitate is multi-faceted, achieved through different mechanisms depending on whether meaningful and meaningless actions are performed (Rumiati & Tessari, 2002), or depending on the content to be imitated (Subiaul, 2016). Other approaches emphasize a domain-general view of imitation, where the copying of actions can be facilitated through the development of associations between motor actions and sensory information (Brass & Heyes, 2005; Prinz, 1997; Ray & Heyes, 2011).

Issues of domain-general versus domain-specific imitative mechanisms are often reflected in the disagreements over the ontogeny of imitative behavior. A strong nativist view assumes that the correspondence problem is solved through an innate specialized mechanism for imitation (Meltzoff & Moore, 1997); a view supported by evidence that newborns can imitate facial expressions (Meltzoff & Moore, 1977). However, evidence of neonatal imitation has come under growing scrutiny over the last few years (Oostenbroek et al., 2016; although see Meltzoff et al., 2017). Proponents of domain-general accounts of imitation have examined multiple avenues of research to support the notion that imitation is largely driven by experience. Heyes and Ray (2000) have proposed the associative sequence learning (ASL) model, which suggests that the cortical connections mediating the observation of the action and the motor activation (or vertical associations) are formed by correlated experiences of observing and performing the same action. In other words, these cortical connections would be formed during associative learning. An individual forms a sensorimotor link for a given action X when the observation and execution of this action X occur in a congruent or correlated manner, that is, when the sensory representation of X is active at the same time as the motor representation of X and not that of another motor action Y. While both nativist and experiential theorists acknowledge the role of genetics and experience in imitative behavior, they propose different pre-existing mechanisms. For example, Meltzoff and Moore's (1997) active intermodal mapping (AIM) theory describes an innate mechanism specifically evolved to match observed movement to specific organs. This supramodal representation system compares perceived actions to proprioceptive feedback from one's own actions to facilitate imitation. Overall, key differences between AIM and ASL accounts include the form of the mechanism used to facilitate imitation (i.e., an amodal representation system vs. a modal sensorimotor system), and the origin of these systems (i.e., supramodal representation systems are thought to exist from birth, while sensorimotor associations develop through experience). Further, while

AIM proposes a domain-specific system adapted for imitation, experiential approaches place domain-general learning mechanisms at the root of imitative behavior that may be scaffolded by species-specific motivational and emotional predispositions (Heyes, 2018).

Studies of automatic imitation have shed light on the mechanisms involved in imitative behavior. Automatic imitation is a kind of stimulus–response compatibility (SRC) effect in which the characteristics of a behavioral performance (speed, accuracy) are mediated by the congruence between a stimulus and an individual's response (Eimer, 1995; Heyes, 2011): It is easier for an individual to perform the same action as a demonstrator than the other way around, even if this may compromise the completion of a task. This type of SRC protocol is commonly used in imitation studies because it is thought to reflect an imitative mechanism. It also allows the isolation of certain processes involved in the transferal of sensory information into a motor action, while minimizing the demands on executive functions. A classic procedure with humans involves a cueing or imperative stimulus (i.e., a green dot for an open hand; red dot for a closed hand) while simultaneously presenting distractor images that are compatible or incompatible with the action to be performed. Using this framework, Stürmer, Aschersleben, and Prinz (2000) showed that adult participants were faster when they had to respond to the color stimulus when the same movement was simultaneously presented (compatible condition) than when the opposite movement was present (incompatible condition). This difference in response time (RT) suggests that observing a stimulus facilitates a compatible response and that one must inhibit this response under incompatible conditions resulting in longer RTs.

Stimulus–response studies involving training or other types of experience have contributed to support for domain-general accounts of imitation. For example, recent studies have shown that children who suffered from bilateral cataract at birth or a few months later and therefore lacked the experience necessary for the potential formation of sensorimotor connections, showed an impaired automatic imitation effect in an SRC task a few months after regaining vision (McKyton, Ben-Zion, & Zohary, 2018). Further, the ASL model predicts that training in situations involving incongruent sensory and motor representations should cancel or even reverse this automatic imitation effect. In other words, if an individual is taught to respond to an "open hand" stimulus with a closed hand, there should be a new connection between an "open hand" visual representation and a "closed hand" motor representation. Incompatible training suggests the emergence of "counter-mirror" neurons that may inhibit the bidirectional link between open-handed sensory and open-handed motor representations, thereby reducing the bias of RT in compatible trials (e.g., Catmur et al., 2008). In a study with adults, incompatible training (in which participants had to open their hands in response to a closed hand stimulus and vice versa), abolished the automatic imitation effect previously observed (Heyes, Bird, Johnson, & Haggard, 2005). Twenty-four hours after this training, responses to incompatible trials were as fast as responding to compatible trials for subjects with incompatible training, compared to subjects with compatible training. Gillmeister, Catmur, Liepelt, Brass, and Heyes (2008) reported a similar abolition of the automatic imitation effect on foot or hand action following incompatible training.

SRC paradigms have also been used to study imitation across a range of non-human species. Mui, Haselgrove, Pearce, and Heyes (2008) found that budgerigars that had to "counter" imitate to get a reward, that is, peck after seeing a stepping stimulus (and vice versa), made significantly fewer correct responses than budgerigars that had to imitate to receive food, that is, peck after seeing a pecking stimulus (and vice versa). Range, Huber, and Heyes (2011) found the same automatic effect but also showed that dogs from the incompatible group (those rewarded for responding with muzzle use after observing paw use and paw use after observing muzzle use) tended to make more errors when presented with compatible trials (i.e., rewarded for using the same body part as a demonstrator in a trial) than dogs from the compatible group. This suggested that dogs in the incompatible group developed a tendency for "automatic counter-imitation," consistent with the sensory–motor models. Finally, although studies involving non-human primates are particularly important because of their phylogenetic proximity to humans, to our knowledge, only one study has examined automatic imitation in an SRC task with non-human primates, showing an SRC effect in capuchin monkeys (O'Sullivan, Claidière, & Caldwell, 2017). Moreover, after counter-imitative training, the authors showed that sensorimotor learning could eliminate the imitative bias, in line with what had already been found in previous experiments with humans and dogs. However, the results of this study remain difficult to interpret due to the small number of individuals studied.

In general, experience-dependent accounts of imitation are underexplored in primate literature, with many studies focusing on identifying imitation at single timepoints to draw conclusions regarding the presence/absence of this ability in a particular species (e.g., van de Waal & Whiten, 2012; Voelkl & Huber, 2000). As described above, in humans, studies have used SRC paradigms to demonstrate the role of experience in imitative responses across a range of effectors and context (e.g., Catmur, Mars, Rushworth, & Heyes, 2011; Press, Gillmeister, & Heyes, 2007). Another method of examining domain-general versus domain-specific accounts is to compare social and asocial learning on the same task. For example, Blandin and Proteau (2000) found that experience obtained through social observation produced similar results to conditions where participants were able to practice the task individually, suggesting the mechanisms underlying imitative behavior were similar to those used in individual learning. In the non-human primate literature, ghost controls are used to assess social learning performance in comparison to asocial learning (i.e., affordance learning, goal emulation; Hopper, 2010). In ghost-control studies, the social information that would normally be available in a social learning trial (i.e., an animal moving a particular object) is instead performed by a non-social agent (i.e., hidden string moving an object). In touchscreen tasks with rhesus macaques (*Macaca mulatta*), ghost controls have been used to demonstrate that in some contexts, the presentation of social information by a conspecific lead to improved learning of a task, when compared to conditions where the same information is presented automatically in some other asocial ways (Subiaul, Cantlon, Holloway, & Terrace, 2004). In a more recent study with capuchin monkeys (*Sapajus apella*), however, no difference was identified between the social and asocial conditions in a touchscreen task (Renner, Kean, Atkinson, & Caldwell, 2021). The impact of social information in touchscreen tasks with non-human primates, then, is currently unclear.

The objective of the present experiment was to explore imitative biases in another non-human primate species, Guinea baboons (*Papio papio*). To our knowledge, there is limited evidence of imitative capacity in this species, and so one of our main objectives was to determine whether there is an imitative bias in this species using a touch screen social learning task. Multiple forms of imitation have been described in the literature (see Subiaul, 2016), but here our task overlaps in terms of goal, action, and cognitive demands, and so we can only draw conclusions regarding general social learning mechanisms (rather than specific forms of imitation—e.g., see Subiaul, 2010). Second, the role of experience in imitation in non-human animals is underexplored, and here we hope to further our understanding of the impact of experience by examining both imitative and counter-imitative behavior. To meet this goal, we used a novel, automated touchscreen task to examine the learning of both rule types across thousands of trials. This method allows us to examine change in stimulus–response learning across time, examining learning across both compatible and incompatible conditions. Finally, we wish to examine whether the presence of another individual has an impact on imitative learning. To address this goal we used a control condition in which there was no social component included in the demonstration (i.e., the demonstrator of the action is replaced by a "ghost" agent (Hopper, 2010); see the Method section). Even though imitation is a form of social learning and therefore necessarily involves the presence of another individual, studies of imitation using SRC in animals have not attempted to show the importance of the presence of others. Even domain-general accounts of imitative learning stress that imitative learning must be built upon a species' capacity to form specific associations between stimuli and responses, which may be scaffolded by motivational biases to attend to social stimuli. It may be possible to demonstrate that SRC effects could be observed in the absence of another individual, which would strongly question the value of the SRC protocol for the study of a special imitative capacity (Ferrucci, Nougaret, Brunamonti, & Genovesio, 2019; Nougaret, Ferrucci, & Genovesio, 2019).

2. Method

2.1. *Participants*

Six males and 13 females Guinea baboons (*P. papio*) were tested in this study (mean age: 11.5 years [min = 2.5; max = 24.6]). They belonged to a social group of 19 individuals living in a 25 x 30 m outdoor enclosure connected to a 6 x 4 m indoor enclosure and two 8 x 4m trailers (Fig. 1a). The monkeys had *ad libitum* access to 10 Automated Computer Learning Devices for Monkeys (ALDMs; Bonté, Flemming, & Fagot, 2011; Fagot & Paleressompoulle, 2009), four in the first trailer and six in the second. The ALDM used an automatic radio frequency identification device implanted in each forearm of the monkeys to recognize the individuals. This device makes it possible to test the animals without having to capture and isolate them.

2.2. *Social (S-ALDMs)*

The ALDMs were connected in pairs to allow an individual in one ALDM to see the touchscreen of the neighboring ALDM (see Fig. 1b; we dubbed this new version of the ALDM

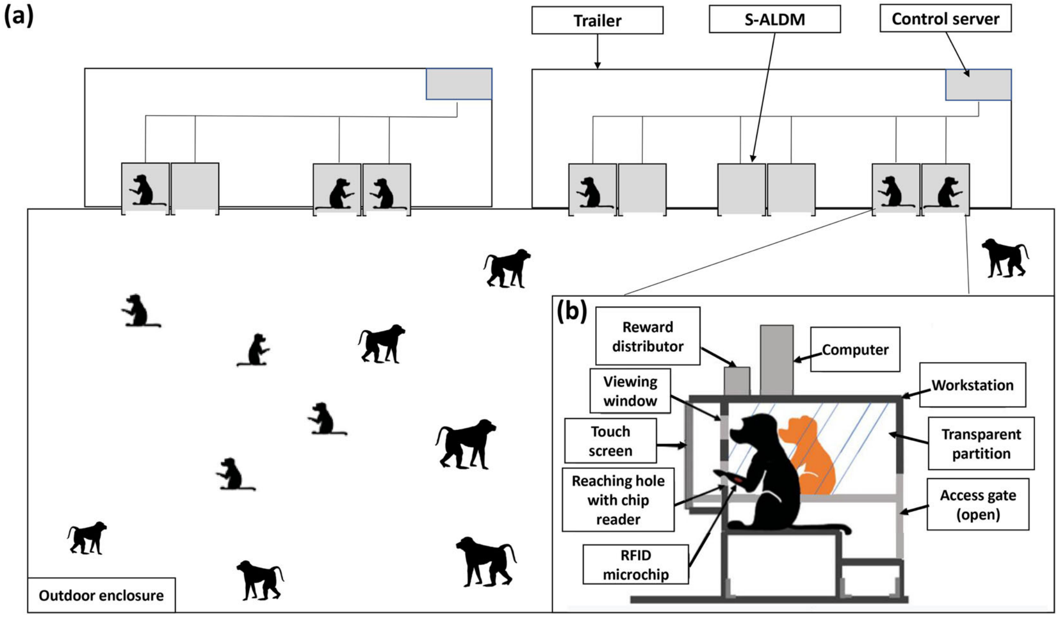

Fig. 1. (a) Nineteen baboons living in an enclosure have *ad libitum* access to two trailers, each containing several social-Automated Computer Learning Devices for Monkey (S-ALDM)-operating conditioning systems. The diagram shows the two bungalows and the five units. (b) Detail of the organization of an S-ALDM, where two monkeys can work side by side, while seeing each other.

system as S-ALDMs; see videos). Two individuals could therefore see each other and their responses on the screen when a transparent partition between the ALDM was used. All the monkeys had previously participated in studies using this ALDM testing system, but the current task was entirely novel.

We used two different tasks, one when two individuals are present, the "dual task," and one when an individual is alone, the "single task." These two tasks are presented below. When a monkey entered an ALDM, a blue screen was displayed with a four seconds delay. If another individual was detected in the neighboring ALDM during this delay, a blue screen was also displayed, announcing the synchronization of the two machines and the start of the dual task (Fig. 2). If the neighboring ALDM stayed empty for four seconds, the single task started.

2.3. Dual task

The dual task (Fig. 2), which is the main focus of this paper, used an SRC paradigm to test the capacity of baboons to learn from a demonstrating partner. In the social version of the SRC task, the test program identified the two monkeys when they entered an S-ALDM, synchronized the two computers, and displayed a blue fixation cross at the bottom center of the screen (Fig. 2b). The test started once both monkeys had pressed the fixation cross within four seconds (otherwise the trial was aborted and re-presented). In each trial, one monkey was randomly selected as the "demonstrator" and would do the first phase of the trial. Two stimuli

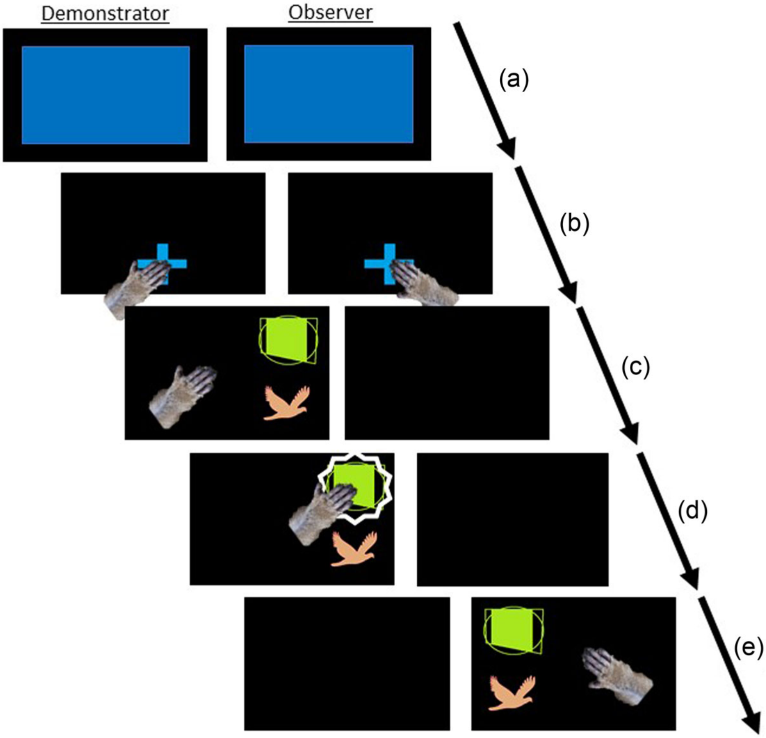

Fig. 2. Schematic representation of the automated dual task on touch screen. The stimulus circled in white flashes briefly when selected. (a) to (e): Succession of events. (a) Each trial, one monkey is randomly selected to be the demonstrator, the other the observer. (b) Each monkey has to first touch a fixation cross. (c) Two randomly selected stimuli selected from a set of 70 appear on the side of the screen at a random (top or bottom) position. (d) When the demonstrator touches one of the two stimuli, it flashes briefly, then the stimuli disappear. (e) the same stimuli, in the same position, appeared on the observer's screen that had to touch the stimuli that were touched by the demonstrator to be rewarded in the compatible condition and the opposite stimuli in the incompatible condition.

were randomly selected from a set of 70 stimuli and were displayed on the screen of the demonstrator monkey (Fig. 2c). These stimuli were located on the side of the screen closest to the adjacent ALDM so that the second monkey had the best possible visibility. Once the stimulus was selected by the demonstrator, it would flash twice (Fig. 2d), then both stimuli would disappear from the demonstrator's screen and appear on the observer's screen, in the same location. The observer then had to choose one of the two stimuli according to what the neighbor had chosen (Fig. 2e). Monkeys were randomly assigned to the compatible or incompatible condition before the start of the experiment (we balanced the assignment of the monkeys in terms of age and sex). Monkeys in the compatible condition had to select the same stimulus as the demonstrator to get a reward. Monkeys in the incompatible condition had to select the opposite stimulus to obtain a reward. The selection of a stimulus toward the bottom of the screen or toward the top of the screen thus led to the performance of two different arm movements (Fig. 3). Note that two monkeys assigned to two different conditions could still

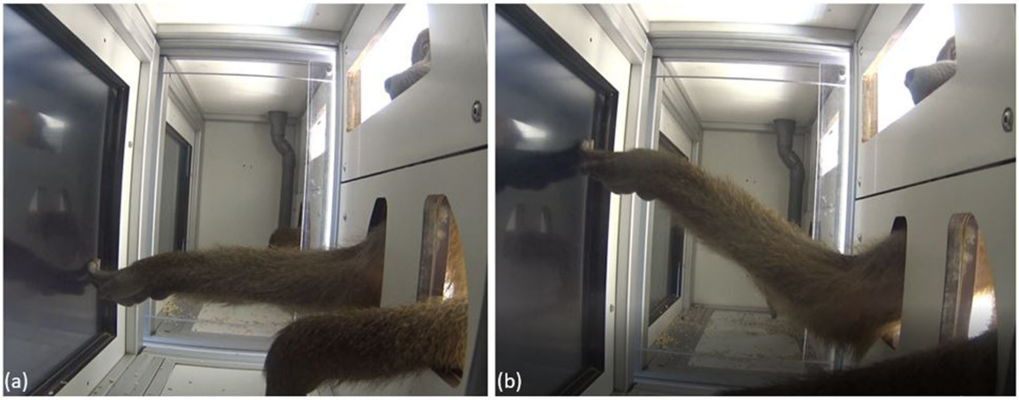

Fig. 3. Stills from a video recorded during the social reversal learning phase of a monkey choosing the stimulus at the bottom (a) or the top (b) of the screen.

take part together since the condition was relevant only to the observer, not the demonstrator. The time in milliseconds (ms) between the end of step (d) and the end of step (e) was used as RT. The success of a test was coded as a binary variable: correct response = 1 and incorrect response = 0. For the demonstrator, any choice made by the observer triggered the delivery of a reward. For the observer, a successful response triggered the delivery of a reward, a miss resulted in a 3 s timeout.

Unlike previous studies on the automatic imitation effect in animals, we used a SRC protocol involving a visual device and the selection of stimuli on a screen. Importantly, the monkeys are used to work on these screens on visual tasks, and therefore, according to the experience-dependent model of imitation (e.g., the ASL model; Ray & Heyes, 2011), they should have formed bidirectional sensorimotor links associated with the use of their arm/hands to touch the screen. Thus, we can expect that the observation of a monkey making a gesture toward a region of the screen will lead to better performances in an observing monkey that has to make the same gesture, compared to a monkey that has to make the opposite gesture.

2.4. *Ghost task*

In addition to the social condition, we introduced a ghost condition that was identical to the social condition as possible. In this condition, one ALDM for each pair of test systems (S-ALDM) was closed and therefore inaccessible (one monkey could enter the pair and see the two screens, but no one could enter next to them). When a monkey entered the opened ALDM, the task proceeded exactly as in the social phase, but all the actions of the neighboring device were automatically performed by the computer. In each trial, the participant was randomly assigned to the observer or demonstrator role to preserve the similarity between the social and the ghost phases. In other words, when the monkey was selected as the observer, the neighboring computer first selected a random stimulus that flashed before the monkey made its choice. When the monkey was selected as the demonstrator, the neighboring computer waited for the demonstrator to choose a stimulus before selecting a random response. The computer's RT was randomly selected from a uniform distribution based on the median RT of the monkeys in the initial social phase (900 ms +/− 450, i.e., [450,1350]).

2.5. *Stimuli and position bias avoidance procedure*

To avoid systematic responses from the demonstrator, such as always choosing the same kind of stimuli (e.g., round vs. spiky), we selected 70 stimuli with similar salience from a set of 1000 (the selection procedure for the stimuli is available in Electronic supplementary material (ESM)). To avoid systematic responses based upon position (i.e., bottom or top of the screen), we also limited to three the number of times the demonstrator could choose the same position in consecutive trials. After the fourth choice in the same location, following trials were considered a miss on the part of the demonstrator until the position changed and the demonstrator's screen immediately displayed a three seconds timeout.

2.6. *Single task*

If a monkey presented itself at the workstation alone and no other monkey participated in the task in the neighboring workstation (at the time of synchronization of the blue screens, see Fig. 2a), a version of the Wisconsin Card Sorting Task (Berg, 1948) was presented. In the task, a monkey could choose between three stimuli combining three colors and three shapes. Reward reinforcement allowed the monkeys to deduce the rule associated with the properties of the stimulus (for instance, round). When an individual reached 80% success in a block of 60 trials, the rule switched, and perseverance was measured by the number of times the individual continued to choose according to the old rule. Using this secondary task allowed the monkeys to maintain their motivation to participate in the experiment while retrieving interesting data on cognitive flexibility. We collected 1,110,770 trials using this task, and since it was a well-known task, we did not expect any relationship between performance on this "single task" and the main study. *Post hoc* inspection of the results did not reveal any pattern, and therefore these data will not be further analyzed in the context of this paper.

3. Experimental timeline

The 19 baboons were divided into two groups (compatible and incompatible), homogenized according to their age, sex, and level of participation in the experiments (see details in T1/ESM). All monkeys followed the same experimental procedure, and all went through the same social and ghost phases.

3.1. *Phase one and two: Initial social and initial ghost tests*

To determine any predisposition for a compatible or incompatible response, the two groups of monkeys carried out a first social phase followed by a ghost phase without changing conditions. If the monkeys had no prior bias, there should be no difference between compatible and incompatible conditions. In these first two phases, we collected a comparable number of trials when the monkeys were observers ($N = 4850$ in the initial social phase, and $N = 6900$ in the initial ghost phase for $N = 7$ monkeys) for a comparable experimental duration (5 days).

3.2. Phase three: Social reversal learning phase

After these first phases, we introduced a "social reversal-learning" phase, during which monkeys alternated between compatible and incompatible conditions upon reaching a predefined criterion of 80% success on 50 trials. The objective of this phase was to evaluate the effect of long exposure to the task on compatible and incompatible responses. Unfortunately, this phase began 2 weeks before the announcement of the coronavirus disease of 2019 (COVID-19) pandemic containment measures. During this 16-day period, we collected 46, 350 observer trials ($N = 7$ monkeys). The experiment started again three months later, after the confinement, and we collected 72,702 observer trials ($N = 7$ monkeys) and 86,788 demonstrator trials over an additional 27 days.

3.3. Phase four: Ghost reversal learning phase

After the social reversal phase, we performed a ghost reversal phase using the same criterion as before. The baboons performed 71,719 observer trials and 82,198 demonstrator trials over 20 days, a number comparable to the after-shutdown social reversal phase. All monkeys started the ghost phase in the condition they were in at the end of the social reversal phase. Another possibility would have been to use the condition they were in at the beginning of the social reversal phase, but since different monkeys had performed a different number of reversals, some monkeys would have started in the same condition and others in a different condition.

4. Statistical analysis

The main objective of the statistical analyses was to determine the influence of the experimental phase (social vs. ghost) and the condition (compatible vs. incompatible) on performance in the task (score and reaction time were analyzed separately). To take into account interindividual variability and repeated measurement, we used mixed models including a random intercept and slope (represented by the number of blocks of 50 trials performed) for each individual (all the model details are presented in the ESM). Thus, we limit our analysis to complete blocks of 50 trials. The score was coded as a binary variable (success = 1, failure = 0), and we averaged it over each block of 50 trials to get the mean score.

Moreover, since the first objective of the experiment was to study variation in performance depending on condition (compatible–incompatible) and how it would vary after training in the opposite condition, we chose *a priori* to analyze the scores of monkeys having reached the threshold at least twice (e.g., a monkey starts in compatible condition, reaches the threshold, switches in incompatible condition and reaches the threshold again) ($N = 7$). Given the small number of individuals who succeeded at the task, it was not possible to analyze the effect of age or sex in any detail but as can be seen in Table 1, there is no obvious pattern.

Table 1
Course of the experiment for the 19 monkeys across the four phases (initial social, initial ghost, social reversal learning, and ghost reversal learning)

Name	Initial Social Phase	Initial Ghost Phase	Social Reversal Learning Phase						Ghost Reversal Learning Phase	
			Number of Reversal						Number of Reversal	
			0	1	2	3	4	5	0	1
Bobo	Compatible *(1)	*(0)	*(56)						*(5)	
Atmosphère	Compatible *(2)	*(1)	*(47)						*(39)	
Feya	**Compatible *(14)**	***(1)**	***(28)**	***(65)**	***(77)**	***(4)**			***(101)**	
Arielle	Compatible *(10)	*(2)	*(239)						*(167)	
Lips	**Compatible *(13)**	***(22)**	***(39)**	***(150)**	***(58)**				***(115)**	***(17)**
Mako	**Compatible *(9)**	***(28)**	***(61)**	***(95)**	***(55)**				***(35)**	***(41)**
Muse	**Compatible *(11)**	***(18)**	***(16)**	***(33)**	***(50)**	***(60)**	***(52)**	***(34)**	***(103)**	
Felipe	Compatible *(3)	*(1)	*(98)						*(1)	
Petoulette	Compatible *(2)	*(0)	*(13)						*(25)	
Ewine	**Compatible *(23)**	***(7)**	***(198)**	***(140)**					***(180)**	
Number of monkeys that reached each reversal phase			10	5	4	2	1	1		
Pipo	Incompatible *(1)	*(0)	*(20)						*(3)	
Kali	Incompatible *(2)	*(0)	*(26)						*(20)	
Fana	**Incompatible *(12)**	***(5)**	***(205)**	***(24)**					***(73)**	
Violette	**Incompatible *(27)**	***(16)**	***(122)**	***(153)**	***(32)**				***(206)**	
Mali	**Incompatible *(9)**	***(27)**	***(63)**	***(88)**	***(47)**				***(88)**	
Lome	**Incompatible *(14)**	***(26)**	***(3)**	***(25)**	***(37)**	***(38)**	***(26)**	***(30)**	***(5)**	***(50)**
Nekketsu	**Incompatible *(6)**	***(13)**	***(31)**	***(137)**					***(76)**	
Harlem	Incompatible *(6)	*(13)	*(136)						*(23)	
Angele	Incompatible *(4)	*(3)	*(73)						*(23)	
Number of monkeys that reached each reversal phase			9	5	3	1	1	1		

Note. The monkeys started either in compatible condition (blue) or in incompatible condition (red). Numbers represent the number of 50 trials blocks performed in each condition. Empty cells mean they have not reached this stage of the experiment. In bold: Monkeys that reached at least once the success threshold.

The effect of the predictors on the score was evaluated using a generalized linear mixed model (GLMM; Baayen, 2008) with binomial error distribution and a logit link function. Models were developed using the glmer function of R’s lme4 package (Bates, Kliegl, Vasishth, & Baayen, 2015). We selected the compatibility condition, and its interaction with the number of blocks performed, as fixed predictors of interest. We set the intercept at trial block zero and at the incompatible condition. The effect of the predictors on the RT was evaluated using a linear mixed model of similar structure to the one used for the score. Because we were interested in how the action of a demonstrator could affect the speed with which the observer did the same action, we only analyzed RTs from successful trials, and we filtered RTs (+/− 2 *SD*s) to avoid biasing the models with overly large distributions.

During our analysis, we faced singularity problems despite our relatively simple random-effects structure containing only a random intercept and slope. There seems to be no agreed-upon solution to this problem, and guidelines recommend achieving a balance between reducing the complexity of random factors to achieve convergence and risking finding spurious effects (Bates, Mächler, Bolker, & Walker, 2015). In our case, the baboons show some systematic interindividual variability (see Fig. 6 below for instance), and we found that model estimations were more realistic using the intercept plus slope random effects rather than just a random intercept (despite the singularity). We, therefore, chose to present the results of the models with the full random effects. All analyses were done with the statistical software R (R Core Team 2020)

5. Results

The experiment lasted 73 days, during which the 19 baboons performed a total of 523,403 dual-task trials (an average of 984 trials/monkeys/day, [min average = 124 trials/day; max average = 2174 trials/day]), of which 240,619 were conducted as observers (on average 46% of the total number of trials [min = 44%, max = 47%]). This is less than expected by chance (binomial test, $p < .001$) and suggests that monkeys were more likely to give up on a trial when they were observers. During the social reversal phase, 10 monkeys passed the criterion of 80% success in a block of 50 successive trials. After changing their condition, seven among them reached the threshold a second time.

Regarding RTs, we noticed that the laboratory’s shutdown had little impact on the score but affected RTs significantly (see Fig. 4, and we provide more details in S1/ESM). Since most of the monkeys had already reached the success criterion once (first reversal), we decided to analyze the RTs of these monkeys before and after the first reversal but not beyond the break. Because we wanted to compare the evolution of RTs over an identical period (same number of blocks) before and after the first reversal, we did not analyze the two entire periods. We had to choose a number of blocks to analyze that on the one hand would represent the number of blocks needed to reach the success threshold before the reversal, but on the other hand, would also avoid including the disruption of the RTs following the shutdown. Therefore, we set the number of blocks at 39 (the median number of blocks for monkeys to reach the first success threshold). Because we could only analyze RTs before and after the first reversal,

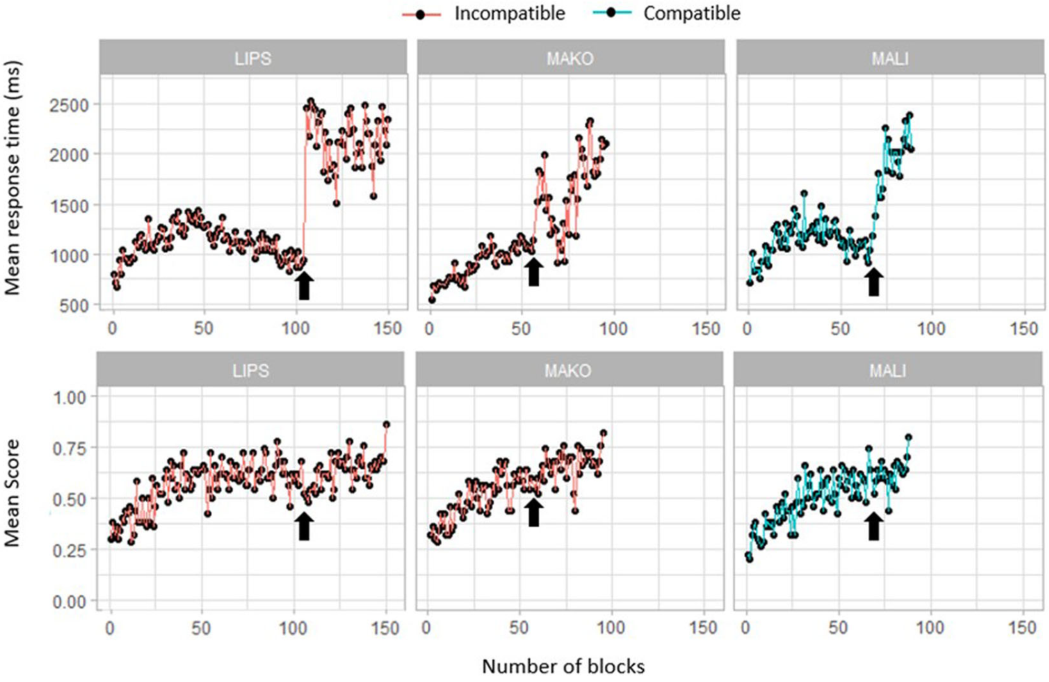

Fig. 4. Average response time (RT) and score of three monkeys impacted by the closure of the platform after they had reached a first success threshold. Black arrow: Closure of the platform; red line: Incompatible condition; blue line: Compatible condition.

we decided to perform the following analyses on the 10 monkeys that reached the success threshold at least once.

6. Phase one and two: Initial social and initial ghost tests

The purpose of the first two phases was to estimate the presence of a bias between the compatible and the incompatible groups.

The results of the analysis showed a slight interaction between the experimental condition (compatible–incompatible) and block number (GLMM, *Condition* x *Number of Blocks*, $\beta = -0.08$, $SE = 0.04$, $z = -1.98$, $p = .047$). The score increased in the incompatible condition ($\beta = 0.09$, $SE = 0.03$, $z = 3.05$, $p = .002$) but not in the compatible condition ($\beta = 0.01$, $SE = 0.03$, $z = 0.55$, $p = .58$), and the score in the incompatible group was significantly higher at the beginning of the phase ($\beta = -0.65$, $SE = 0.23$, $z = -2.832$, $p = .005$) than in the compatible group. Looking at reaction times, we found no interaction between condition and number of blocks (LMM, $\beta = -0.45$, $SE = 14.98$, $t = -0.03$, $p = .98$). Initially, monkeys were faster in the incompatible condition ($\beta = 291.64$, $SE = 125.68$, $t = 2.32$, $p = .02$), and RT decreased with the number of blocks in both conditions (compatible: $\beta = -21.5$, *SE* = 8.34, $t = -2.58$, $p = .01$; incompatible: $\beta = -25.81$, *SE* = 11.23, $t = -2.3$, $p = .02$), a result typical of such experiments where monkeys become faster over the time.

During the initial ghost condition, the results showed a small interaction between the condition and block number on scores (GLMM, $\beta = 0.04$, *SE* = 0.021, $z = 2.03$, $p = .04$). The score in the incompatible group decreased ($\beta = -0.04$, *SE* = 0.015, $z = 2.29$, $p = .02$) while it stayed stable in the compatible group ($\beta = 0.002$, *SE* = 0.014, $z = 0.48$, $p = .63$), and they were no initial difference at the beginning of the phase ($\beta = -0.59$, *SE* = 0.43, $z = -1.37$, $p = .17$). Regarding reaction times, we found a significant interaction between condition and number of blocks ($\beta = -15.39$, *SE* = 6.34, $z = -2.43$, $p = .015$). RTs increased in the incompatible group ($\beta = 13.26$, *SE* = 4.5, $t = 2.94$, $p = .003$) but not in the compatible group ($\beta = -2.13$, *SE* = 4.5, $t = -0.48$, $p = .63$). Moreover, RTs were faster in the incompatible group at the beginning of the phase, compared to the compatible group ($\beta = 207.9$, *SE* = 94.97, $t = 2.19$, $p = .028$).

Taking a closer look at the individual results, we noticed that Lome, a monkey that had quickly reached an accuracy score of 80% during the initial social phase (in incompatible condition), dropped to 20% success during the ghost phase, and Mali, which also reached a score of 80% during the initial social phase (in incompatible condition), also dropped to 50% success during the ghost phase. The change in behavior of these two monkeys can explain the results of this first phase (further discussed in the ESM/S2/S3). Regarding the other individuals, they showed no evidence of learning the task.

7. Phase three: Social reversal learning

During the social reversal learning phase, seven monkeys (among the group of 19) reached the success threshold at least twice (i.e., performed at least two reversals). Four of them began in the compatible condition. We found no significant interaction between condition and number of blocks in the first reversal phase (*Condition* x *Number of Blocks*: $\beta = 0.008$, *SE* = 0.005, $z = 1.59$, $p = .11$), indicating that the two groups learned at a similar speed. There was also no evidence of an initial difference between the condition ($\beta = -0.31$, *SE* = 0.2, $z = -1.53$, $p = .13$). The average score of monkeys in the incompatible condition increased at an estimated rate of $\beta = 0.010$ (*SE* = 0.006, $z = 1.706$, $p = .09$), while it increased in the compatible condition at an estimated rate of $\beta = 0.019$ (*SE* = 0.005, $z = 3.802$, $p < .001$; Fig. 5).

Regarding reaction times (Fig. 6a), we found no interaction between the condition and the number of blocks ($\beta = -2.28$, *SE* = 3.6, $t = -0.63$, $p = .53$), there were no initial difference between the RTs in both condition ($\beta = 106.36$, *SE* = 78.4, $t = 1.35$, $p = .18$). RTs were stable during this phase in incompatible condition ($\beta = -2.9$, *SE* = 2.62, $t = -1.12$, $p = .26$) and increased slightly in the compatible condition ($\beta = -5.2$, *SE* = 2.48, $t = -2.1$, $p = .04$). Furthermore, when we averaged RTs for each monkey during this phase, we found no clear evidence of a difference between conditions ($N = 10$, $t = -1.86$, *df* = 7.72, $p = .10$).

After reaching the first 80% success threshold, seven monkeys changed condition and entered the second reversal. We found no significant difference in the evolution of the

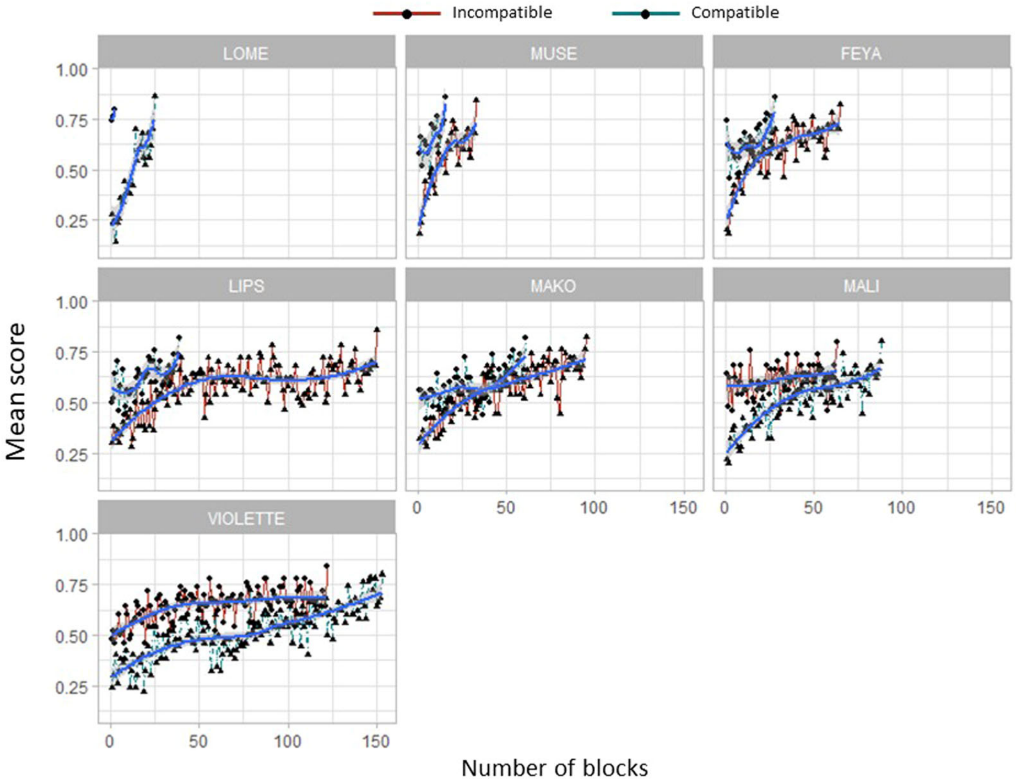

Fig. 5. Mean score in incompatible (red) and compatible (blue) conditions, before (circle) and after (triangle) the first reversal, for the seven monkeys that performed at least two reversals. Blue lines represent the local regression (locally estimated scatterplot smoothing (LOESS) method).

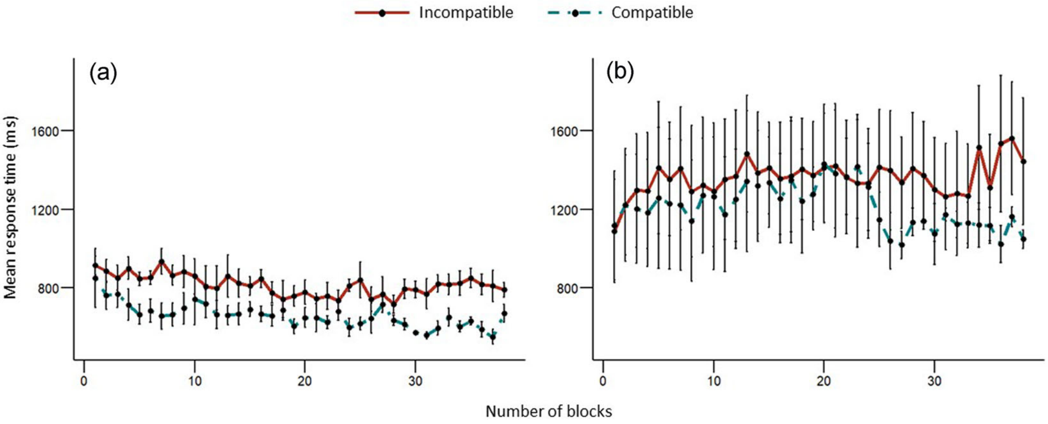

Fig. 6. Mean RT in the incompatible (red solid line) and compatible (blue dotted line) conditions during the social reversal learning phase before (a) and after (b) the first reversal. Error bars represent the standard error of the mean.

monkeys' scores during the second reversal (*Condition* x *Number of Blocks*, $\beta = 0.014$, $SE = 0.022$, $z = 0.669$, $p = .5$). However, we found an initially slightly higher average score in the incompatible condition ($\beta = -0.43$, $SE = 0.2$, $z = -2.16$, $p = .03$), and the average score of monkeys in the incompatible condition increased at a rate of $\beta = 0.024$ ($SE = 0.014$, $z = 1.75$, $p = .08$) and at a rate of $\beta = 0.039$ ($SE = 0.016$, $z = 2.37$, $p = .018$) in the compatible condition.

In the first 39 blocks after the first reversal (Fig 6b), we found no interaction between the condition and the number of blocks ($\beta = 10.3$, $SE = 6.19$, $t = 1.66$, $p = .1$), and there was no initial difference between the RTs in both condition ($\beta = -165.7$, $SE = 429.2$, $t = -0.39$, $p = .7$). Furthermore, RTs were stable during this phase in both conditions (compatible: $\beta = 8.07$, $SE = 4.39$, $t = 1.84$, $p = .066$; incompatible: $\beta = -2.2$, $SE = 4.36$, $t = -0.5$, $p = .61$). Similarly, we found no difference between averaged RTs ($N = 10$, $t = -0.14$, $df = 7.99$, $p = .89$).

After the second reversal, the seven monkeys changed condition again, and we found no significant effect of the condition on the learning of the task ($\beta = -0.002$, $SE = 0.009$, $z = -0.265$, $p = .79$), we found no initial difference between the two conditions ($\beta = -0.15$, $SE = 0.11$, $z = -1.31$, $p = .19$), and the score progressed at a similar rate in the two conditions (compatible: $\beta = 0.02$, $SE = 0.006$, $z = 3.73$, $p < .001$; incompatible: $\beta = 0.02$, $SE = 0.007$, $z = 3.35$, $p < .001$).

Note that we cannot directly compare the first reversal to the second (within individuals) because during the first reversal, the monkeys had to learn a condition, while during the second they had to unlearn the first condition and learn the new one. Their learning rate during the second phase was therefore different from the initial learning phase. Only three of the seven monkeys performed a third reversal (Feya, Lome, and Muse), and two continued until they reached five reversals (Lome and Muse; see Table 1). Then, we analyzed separately the results of Lome and Muse and did not find a significant difference between the learning rate in the compatible and incompatible conditions (Lome, $\beta = 0.045$, $SE = 0.03$, $z = 1.40$, $p = .16$ and M*USE*, $\beta = -0.0028$, $SE = 0.011$, $z = -0.258$, $p = .8$; see Figs. S4 and S5).

7.1. Phase four: Ghost reversal learning

In the ghost reversal learning phase, three monkeys (Lips, Lome, and Mako) among the seven monkeys that reached this phase reached the success threshold once. None of the other 12 monkeys, which had the opportunity, reached such criterion. The three monkeys that passed were all in the compatible condition, while none of the four monkeys in the incompatible condition passed. Consistent with this observation, we found a significant interaction between condition and block ($\beta = 0.006$, $SE = 0.002$, $z = 3.89$, $p < .001$) suggesting that monkeys in the compatible condition learned faster than monkeys in the incompatible condition. We found no initial difference between conditions ($\beta = -0.23$, $SE = 0.24$, $z = -0.97$, $p = .33$), but the average score of monkeys in the incompatible condition remained stable ($\beta = 0.0004$, $SE = 0.0004$, $z = 1.21$, $p = .23$), while it increased in the compatible condition ($\beta = 0.006$, $SE = 0.015$, $z = 4.30$, $p < .001$). Furthermore, by comparing the ghost reversal phase with a comparable number of trials at the beginning of each phase of the social reversal phase,

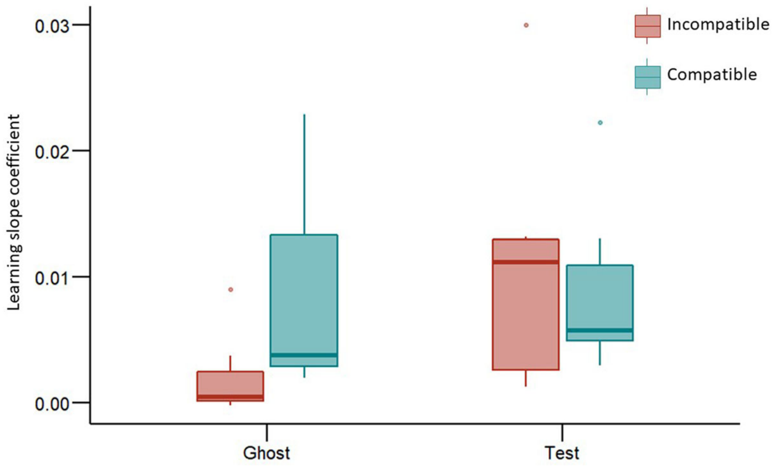

Fig. 7. Distribution of the learning slopes of the seven monkeys that performed both the social and ghost reversal learning phases in incompatible (red) and compatible (blue) conditions.

we found a significant difference between the two phases ($N = 7$, $W = 143$, $p = .01$), monkeys learned faster in the social reversal phase, compared to the ghost reversal phase. Looking at each condition separately, this difference was significant only for the incompatible condition (compatible: $W = 17$, $p = .6$; incompatible: $W = 56$, $p = .008$; Fig. 7).

Since none of the monkeys in the incompatible condition reached the success threshold, we could not compare RTs between the compatible and incompatible conditions of the ghost phase. However, one of the purposes of this study was to determine if the presence of a nearby individual was affecting the RT of the focal participant. The comparison of the first blocks of the ghost and social reversal phase in compatible condition suggests that the monkeys in the social condition have slightly faster RTs than monkeys in the ghost phase (Fig. 8). We found no effect of the interaction between the phase and the number of blocks on the monkey's RT ($\beta = -0.56$, $SE = 0.68$, $t = -0.82$, $p = .41$). We found an initial difference between phases ($\beta = -290.69$, $SE = 15.62$, $t = -18.61$, $p < .001$), but the RTs progressed at a similar rate in both reversal phases (ghost: $\beta = -3.6$, $SE = 2.3$, $z = -1.57$, $p = .12$; social: $\beta = -3.35$, $SE = 1.93$, $z = -1.73$, $p = .08$). When we averaged RTs for each monkey during this phase, we found a small non-significant difference between conditions ($N = 10$, $t = -1.98$, $df = 7.98$, $p = .08$).

These results suggest that the ghost condition had a detectable effect on the incompatible condition, not the compatible one. However, surprisingly, the learning rates of all three successful monkeys remained high after they changed for the incompatible condition. Their learning rates were not significantly different from the rates observed during the social reversal phase ($W = 7$, $p = .28$). Despite this lack of difference at the group level, we did, anecdotally, notice some interesting individual patterns. We found that Lome, the monkey that achieved the success criterion the most times over the entire experiment, took an average of 1100 trials (150, 1850, and 1300) to do so in the incompatible condition during the social

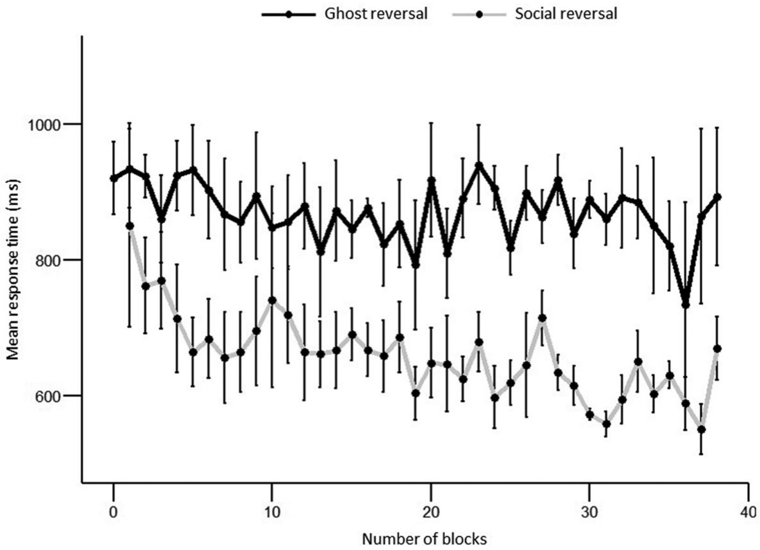

Fig. 8. Mean RT in the compatible condition during the social reversal learning phase (light gray) and the ghost reversal learning phase (dark) before the first reversal. Error bars represent the standard error of the mean.

reversal phase. After reaching the criterion in the compatible condition in the ghost phase, he failed to succeed in the incompatible condition after 2500 trials before the phase ended.

8. Discussion

Domain-general accounts of imitation (e.g., Heyes & Ray 2000; Prinz., 1997) propose that imitation is the result of associative learning during the sensory–motor experience. Domain-specific views on imitation argue that imitative capacities are adaptations to address specific problems (e.g., Subiaul, 2010) but that experience will also guide the development of various social learning skills throughout development (Meltzoff & Moore, 1997). Given the central role of experience under both of these accounts, the main purpose of this study was to examine imitative behavior in baboons in the context of the experience of both compatible and incompatible rules, across social and asocial conditions.

Specifically, we were interested in whether baboons might have initial preferences to imitate behaviors and whether they may learn compatible rules more quickly than incompatible rules and/or reach higher performance (in terms of score and/or RTs). We also wanted to examine whether any differences in performance stay stable over time (i.e., during reversal learning phases). In addition to examining imitative biases, we also wanted to test the importance of the social component of this SRC paradigm, namely, the role of the demonstrator, by contrasting the social condition to a ghost control. Both domain-general and domain-specific accounts predict that learning should be impaired in the ghost condition for social species.

Our results showed that during the initial social phase of testing, the score increased slightly in the incompatible condition but not in the compatible condition. This is likely linked to the fact that two monkeys of the incompatible group quickly reached an average score of 80%. The performance of these two monkeys does not specifically point toward a bias for counter-imitation but is more likely the result of chance factors (i.e., two monkeys that are particularly proficient at this task). In fact, ten monkeys reached the success criterion in the whole experiment, five in each condition. Similarly, we found that RTs were slightly faster in the incompatible condition at the beginning of the experiment, but this small difference is difficult to interpret. Since the scores were very low, this difference is unlikely to reflect a bias for one condition over another. During this phase, RTs decreased similarly in the two conditions as the monkeys gained more experience with the task. During the initial ghost phase, we observed no systematic bias for either condition. We can therefore conclude that initially the monkeys were not biased toward one condition over another in both social and asocial conditions.

During the reversal phases, we found no evidence of a difference in score between the compatible and incompatible conditions, with learning progressing at a similar pace in the two conditions across the reversal phases. Similarly, we did not find a systematic effect on RTs. Monkeys in the compatible condition had a small tendency to be faster than monkeys in the incompatible condition (Fig. 6a), and the absence of a significant difference could be explained by a lack of power, given that only ten individuals participated in this phase and that the difference remains small. Faster RTs in the compatible condition could suggest that seeing the action of a neighboring monkey results in a quicker response for the observer by eliciting the same motor response. However, we note that this difference disappeared after the first reversal (Fig. 6b).

The absence of a difference in score and RTs between the compatible and incompatible conditions stands in sharp contrast to previous studies. Since the first results that have highlighted the “automatic imitation” effect (Brass, Zysset, & von Cramon, 2001), many studies have focused on the mechanisms involved in its properties as well as on its neurological components (Bien, Roebroeck, Goebel, & Sack, 2009; Catmur, Walsh, & Heyes, 2009). Heyes (2011), proposes that automatic imitation would result from a combination of effector and movement compatibility. This is consistent with recent studies suggesting that the mirror neuron system can integrate and represent an entire action, using the multiple components necessary for its realization (Cracco & Brass, 2017; Cracco, De Coster, Andres, & Bras, 2016). Although in humans, most studies on imitation bias have focused on the body part component, faster RTs (between the observation of the action and the motor response) in the compatible condition is a common finding (Bertenthal, Longo, & Kosobud, 2006; Gillmeister et al., 2008; Otte, Habel, Schulte-Rüther, Konrad, & Koch, 2010), and studies have found reliable results for imitation using movement compatibility (Brass et al., 2001; Heyes et al., 2005; Obhi & Hogeveen, 2010). In animals, however, SRC paradigms generally use different body parts (e.g., head or paw with dogs). Studies have shown that it was easier to reach a success criterion in compatible trials in dogs (Range et al., 2011) and capuchins (O’Sullivan et al., 2017) and that budgerigars would do more correct responses in compatible trials (Mui et al., 2008). In contrast to previous research with non-human animals, we used the same body part in both conditions but with different movements (hand raised up or down), and it is possible that biases in copying certain movements are more difficult to capture than actions made with different body parts, even with precise measures of reaction times. This is the first study in non-human animals to examine social learning in an SRC paradigm that has not used different effectors, and so it is possible that in previous studies, the movements examined (peck vs. step—Mui et al., 2008; paw vs. mouth movement—Range et al., 2011; hand vs. mouth action—O'Sullivan et al., 2017) activate different social learning biases than those activated during the copying of spatial/stimulus matching tasks. Therefore, our null findings, when considered alongside successful attempts to identify imitative biases may be consistent with a multi-level approach to copying behavior in animals (Rumiati & Tessari, 2007; Subiaul, 2010).

Nonetheless, methodologies examining the copying of movement in a particular direction or toward certain stimuli have been used across a range of social learning contexts and species (e.g., Aplin et al., 2015; Renner et al., 2021), and so we would expect that social learning biases in this species might drive easier copying of movement in the same direction and toward the same stimulus. The demonstrator and subject were encouraged to perform actions with different hands. This choice was made for practical reasons to improve the visibility of movements; however, it may have influenced the likelihood of observing a compatibility effect. In human SRC studies, mirrored stimuli are often used (i.e., presenting a stimulus image of a left hand when responding with a right hand; e.g., Brass et al., 2001). However, in primates, it may be more important to provide demonstrations that are consistent with the animal's perspective of their own body. For example, it has been suggested that in humans, self-observation of actions is one of the primary means through which the sensorimotor associations that facilitate imitation are formed (Ray & Heyes, 2011; Wiggett, Hudson, Tipper, & Downing, 2011). This may be more important in non-human primates that do not have the same variety of sensorimotor experience to facilitate the development of an imitative capacity (e.g., synchronous behavioral routines, interactions with mirrors, etc; Ray & Heyes, 2011).

In humans, studies have also shown that a short period of counter-imitative training was enough to cancel or to reverse the automatic imitation effect—six blocks of 72 trials in the Heyes et al.'s (2005) study were enough to cancel the automatic imitation effect. In children, when three- to seven-year-olds were asked to perform a different response to a cuing action across only ten trials (i.e., wave when they observed hand clapping), automatic imitation effects in subsequent trials were reduced (O'Sullivan, Berg, & Caldwell, 2018). However, it is difficult to know the extent of rehearsal needed to bring about a reorganization of the sensorimotor representations of an action across different species. Interestingly, we found no systematic evidence of an effect of rule-reversal linked to the compatible/incompatible conditions. The learning speed before and after reversal was very similar in the two conditions (Fig. 5). This suggests that monkeys in our experiment used the same (associative) learning mechanism across the two conditions—whether copying the same movement or moving toward a different location. Another explanation may be that the monkeys were not learning to associate the observed actions with performed actions (i.e., sensory–motor associations, S-M) but learning associations between the locations (or stimuli) selected on the demonstrator display and stimuli/locations on their own display (i.e., sensory–sensory associations, S-S).

We cannot rule this explanation out, and if S-S associations are the primary driver of learning here, this might also explain the differences observed in our paradigm when compared to other comparative work that has used different effectors (which necessitate learning a rule between stimulus and specific motor responses).

It should also be noted that only 10 of the 19 monkeys tested reached the pre-specified threshold once and only seven twice. The introduction of the paired workstations in which baboons can see what another individual is doing is recent (2018), and it appears that some monkeys are still showing difficulties at understanding that they must, in some tasks, look at what the neighbor is doing. This could explain some variability in the initial phase of learning, with certain monkeys, such as Lome, reaching the criterion during the initial phase, while others took much longer. However, all monkeys were equal in this respect after the first reversal.

In general, the monkeys tested here are indeed highly trained in screen-based tasks. We believe that the impact in this experiment may be because the monkeys were highly trained to perform individual tasks, and thus to look at their own screen and not at what their neighbor is doing. It is, therefore, possible that untrained monkeys, or monkeys that we would first train to socio-cognitive tasks, would take less time to learn this, and the potential imitation bias would be quicker to pick up. However, no age effect was observed, young monkeys with less experience with ALDM show identical results to some adult monkeys.

Finally, we wanted to test the relevance of the presence of a demonstrator in the SRC paradigm using a ghost control. First, we note that during the initial testing phase, the scores of the two monkeys that had managed to reach the criterion in the incompatible condition dropped when they entered the ghost phase. Second, during the ghost reversal learning phase, our results show that only three monkeys among nine reached the success threshold and that they all were in compatible condition. The six monkeys in the incompatible condition showed no sign of improvement at all. The monkeys, therefore, exhibited a real difficulty in learning the incompatible condition in the ghost condition (when it is required to pick the opposite stimulus to the one that flashes), whereas they could all do so with a demonstrator. Surprisingly, all three monkeys that learned the compatible condition during the ghost phase started learning the incompatible condition without apparent difficulty after reversal. Although this could be due to chance alone (may be it just happens to be three monkeys that are good at this task), it could also be that the individuals need to first associate the relevant cue (flashing) to their response, and they can do so more easily in the compatible condition. Once the monkeys have learned that the correct response depends on stimulus flashing rather than on other features (such as color, shape, etc), they can then generalize this learning to the incompatible rule.

The fact that the three monkeys learned the compatible rule in the ghost condition is informative. Studies of imitation using the SRC paradigm assume that the presence of a demonstrator is a necessary component of the process. Some studies have shown that human children, apes, and monkeys are capable of learning from a ghost display in touch-screen studies (Ferrucci et al., 2019; Renner et al., 2021; Renner, Patterson, & Subiaul, 2020) or in other social learning studies (Huang & Charman, 2005; Tennie, Call, & Tomasello, 2006; Thompson & Russell, 2004); however, the learning deficit we see in these conditions in non-humans primates in particular (see Hopper, 2010) suggests that monkeys and apes are at a significant disadvantage without the scaffolding afforded by conspecific behavior or mere presence. In humans, a robotic hand can still elicit an automatic imitation effect, although one less potent than a human hand (Press, Bird, Flach, & Heyes, 2005). If the SRC effect exists in the absence of a demonstrator, is it still relevant to imitation? Noticeably, when we compared the social and ghost phases' RTs in the compatible condition, we found a trend toward faster average RTs in the social condition (Fig. 8). This suggests that the movement of the demonstrators elicits a faster response than the flashing cue, but the flashing cue is still effective. It has been reported that Guinea baboons in the wild are tolerant to the presence of conspecifics (Fischer et al., 2017) and it could be that presence of a conspecific leads to quicker actions in foraging and food processing behavior so as to avoid potential competition. For example, while much social learning literature assumes that animals will benefit from copying, in some cases, it is advantageous to perform different or complementary behaviors. Hopewell, Leaver, Lea, and Wills (2010) found that gray squirrels find it easier to learn to choose a pot that a conspecific had not examined over a pot where a conspecific had previously obtained a reward, a finding consistent with gray squirrel foraging behavior. Indeed, here, a bias toward an opposite behavior (or location) may explain some of the significant effects—that is, before taking part in this study, participants may have learned that food rewards are more likely to be obtained when interacting with locations that are different from those explored by conspecifics. While beyond the scope of this study, imitation research driven by an understanding of naturalistic foraging behaviors may shed light on both imitative and counter-imitative biases.

9. Conclusion

Is it easier to do the same action, compared to a different action? We used an SRC task with reversal learning phases in baboons to gain insight into the origins of automatic imitation. We found no clear difference between the compatible and incompatible conditions, although the monkeys tended to be slightly faster in the compatible condition. Remarkably, we found that the learning rates between the two conditions were very similar, even after reversal. These results contrast with what has been previously documented in humans and non-human animals, and it may be due to the use of different movements rather than different body parts. Using a ghost control, we found that monkeys in the incompatible condition experienced important learning difficulties and that monkeys in the compatible condition tended to be slower. These results suggest that the presence of the demonstrator plays a role in eliciting a response but at the same time show that the presence of the demonstrator is not essential, calling into question the relevance of this form of SRC task to study automatic imitation. While the absence of any obvious differences between compatible and incompatible responses makes it difficult to draw conclusions regarding the ontogeny of imitation, this first study of conspecific "automatic imitation" in primates highlights the difficulty in observing imitation in monkeys at all (whether automatic or not).

Imitation is pervasive in human social interactions from a young age fulfilling instrumental and normative functions (Over & Carpenter, 2011), but in monkeys, even the existing evidence of imitative biases are not indicative of strong imitative tendencies (e.g., O'Sullivan et al., 2017; Voelkl & Huber, 2000). Of course, the imitative faculty in primates may not represent one specific cognitive ability. Instead, what has been defined generally as imitation could represent a range of cognitive skills executed to different extents across species, context, and development (Subiaul, 2016). The task we used here may not facilitate strong social learning effects in this species due to these animals' evolutionary or individual histories. Here, we demonstrate the difficulty in observing the presence of bodily imitation in monkeys adding to a literature of failed attempts at identifying imitations in monkeys (see Visalberghi & Fragazy, 2001). In human research, evidence from dozens of studies suggest that automatic imitation paradigms measure imitative tendencies (see Cracco et al., 2018), but there is still some debate over how much automatic imitation is moderated by a more general spatial compatibility effect (e.g., Ramsey, 2018). SRC paradigms are a wonderful means of determining compatibility effects under controlled experimental conditions, and here, our aim was to extend this paradigm to the question of imitation in monkeys. Across thousands of trials, we observe the little impact of imitative or spatial compatibility on task success demonstrating a clear difference in the ways humans and monkeys perform in these paradigms.

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Open Research Badges

This article has earned Open Data. Data are available at https://osf.io/b68x2/.

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Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Fig. S1. Average RT of all monkeys in the social phase showing how they were impacted by the closure of the platform after they had reached a first success threshold.

Fig. S2. Mean score in the incompatible (red) and compatible (blue) conditions in the initial social phase for the seven monkeys that performed at least two reversals during the experiment.

Fig. S3. Mean score in the incompatible (red) and compatible (blue) conditions in the initial ghost phase for the seven monkeys that performed at least two reversals during the experiment. Blue lines represent the linear regression (lm method).

Fig. S4. Mean score of Lome for all the reversals he passed in the social reversal learning phase (from 0 to 5) in compatible (blue) and incompatible (red) conditions. Blue lines represent the linear regression (lm method).

Fig. S5. Mean score of Muse for all the reversals he passed in the social reversal learning phase (from 0 to 5) in compatible (blue) and incompatible (red) conditions. Blue lines represent the linear regression (lm method).

Video