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Six adult male rhesus monkeys did not learn from the choices of a conspecific shown in videos

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Abstract
There is substantial evidence of group-specific behaviors in wild animals that are thought to be socially transmitted. Yet experimental studies with monkeys have reported conflicting evidence on the extent to which monkeys learn by observing their conspecifics. In this study, we tested the feasibility of using pre-recorded video demonstrations to investigate social learning from conspecifics in rhesus monkeys. With training, monkeys gradually learned to respond correctly following videos of a demonstrator, however, follow-up experiments revealed that this was not due to learning from the demonstrator monkey. In generalization tests with videos that were horizontally reversed, monkeys continued responding to the location they had associated with each video, rather than matching the new choice location shown in the mirrored video. When the task was changed to make location irrelevant, such that monkeys could choose correctly only by selecting the same image selected by the demonstrator in the video, observer monkeys did not exceed chance in 12,000 training trials. Because monkeys readily learn to follow nonsocial visual cues presented on a monitor to guide image choice, their inability to learn from a demonstrator here indicates substantial limitations in the capacity for social learning from videos. Furthermore, these findings encourage deeper consideration of what monkeys perceive when presented with video stimuli on computer screens.

Keywords Social learning · Imitation · Video demonstration · Primate cognition · Conspecific imitation

Introduction

There is substantial evidence of animal traditions from field studies (reviewed by Whiten 2021). Yet despite many examples of behaviors thought to be socially learned in wild monkeys, experimental studies with laboratory monkeys have reported conflicting evidence on the extent to which captive monkeys learn novel behaviors by observation (Visalberghi and Fragaszy 2002; Subiaul 2007; Subiaul et al. 2016). Some authors have suggested that monkeys learn novel cognitive rules (Subiaul et al. 2004), and new applications of familiar motor behaviors in novel contexts (Gunhold et al. 2014), but not novel motor behaviors. These findings suggest that a potential key limitation on social learning in monkeys is the type of information made available for transmission through observation. In this study, we tested the feasibility of using pre-recorded video demonstrations to investigate social learning in rhesus monkeys (*Macaca mulatta*). Video-recorded demonstrations offer experimental advantages over field data and live-demonstrator laboratory studies because they allow controlling the information available to the learner. While live demonstrations offer the closest analog to social learning in the wild, previous work has shown that marmosets can learn from videos (Gunhold et al. 2014), and that monkeys can recognize and extract at least limited social information about conspecifics from videos and images (Parr et al. 2000; Pokorny and de Waal 2009; Paxton et al. 2010; Mosher et al. 2011; Adachi and Hampton 2011).

Taxonomies of social learning (e.g., Whiten et al. 2004) typically differentiate between multiple processes that allow animals to learn from others. Only some of these processes involve the learner imitating the behavior of the demonstrator. The experiments described in this manuscript tested whether laboratory-housed rhesus monkeys learned from viewing videos of another monkey solving computer-based tasks. This use of videos could allow for several, but not all, of the social learning processes described by Whiten et al.

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These experiments were designed to test for the presence of any social learning and were not designed to distinguish among specific mechanisms of social learning. We elaborate further on the specific processes that could support social learning in each experiment in the discussion.

We developed a simple paradigm in which monkeys could learn from a conspecific demonstrator shown in a video choosing between two stimuli. We used these video demonstrations to investigate three questions: First, do monkeys spontaneously learn from videos of conspecifics? Second, do monkeys learn to follow video demonstrations more frequently with training? And third, what types of information do the monkeys rely on when they do follow the video demonstrations?

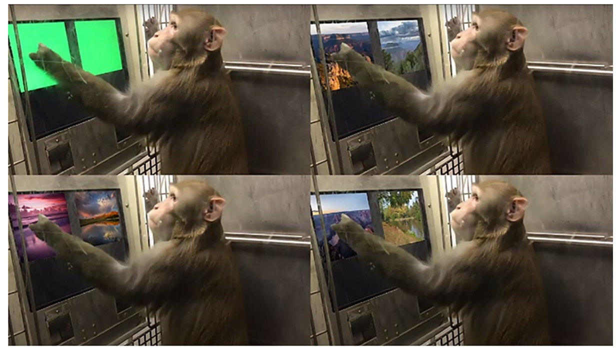

Fig. 1 Video editing process used to generate the video stimuli used. The top left panel shows a still frame from the original unedited footage. The other three panels show the same video after editing to create demonstrations of three different choices

Subjects & materials

Subjects & testing environment

Six adult male rhesus macaques (*Macaca mulatta*, mean age at the start of Experiment 1 = 13.17 years, SD = 1.57), singly housed at the Emory National Primate Research Center were used. Monkeys were reared in natural family groups at the Primate Center field station until about 2.5 years of age, at which point they were moved to a laboratory environment and pair housed. Pair housing continued for many years until the monkeys became socially incompatible and were switched to single housing at the direction of veterinary staff. Monkeys were tested in their home cages, where they had visual and auditory contact with other adult male monkeys.

All 6 monkeys had a long history of cognitive testing but had not been tested previously on a social learning task. Monkeys had experience viewing videos for enrichment outside of testing time, some of which depicted other monkeys or animals. Testing was completed on a touchscreen identical to the one used by the demonstrator monkey (Fig. 1), and custom testing programs were written using Visual Basic. Monkeys worked for food pellets during the day, 6 days per week, and the caloric intake gained from testing was subtracted from each monkey's daily caloric allowance, as determined by veterinary staff before they received their remaining feed at the end of the day. Testing for Experiments 1–5 was conducted over the course of 7 months from August 2020 to March 2021, with other experiments unrelated to social learning occurring between experiments in this study. The replication presented in Experiment 6 was conducted later between August and September of 2021. The time between individual experiments within this study varied by subject, depending on the time each monkey needed to complete other studies.

Video stimuli

We generated the video stimuli for the experiments by recording one of the monkeys responding to one of two "green screen" squares on the same touchscreen used in our experiments (Fig. 1, top-left panel). The demonstrator monkey was recorded responding on both the left- and right-hand side of the screen on different trials, and video clips always ended with a secondary auditory reinforcement and a food pellet being dispensed to the demonstrator monkey. This procedure allowed us to demonstrate a selection of stimuli in the same context in which our subjects would be tested. Four trials were chosen for each response location to generate eight unique video templates. The resulting video templates were each 6 s long.

Statistical analyses

Analyses were conducted using SPSS version 27. Proportion scores were arcsine-transformed using the formula (2*arcsine(sqrt(proportion)) prior to analysis (Aron and Aron 1999). Wherever rANOVA was used, the degrees of freedom were adjusted for sphericity violation using the Greenhouse–Geisser correction.

Experiment 1: monkeys did not spontaneously learn from the choices made by a conspecific demonstrator

Experiment 1 tested whether monkeys spontaneously use videos to learn image discriminations faster than they could by trial and error alone. Monkeys could perform accurately either by memorizing a large set of image discriminations concurrently or by learning from the behavior of the monkey in a video immediately preceding some of the trials. If monkeys spontaneously engage in social learning, then they would respond accurately sooner, and potentially learn image discriminations faster, when discriminations were preceded by a demonstration compared to when they could only learn by trial and error.

Procedure

Monkeys were trained with 260 distinct image-pair discriminations concurrently (520 images; 260 pairs). Two-hundred-eight (80%) of these discriminations were always preceded by a video of the demonstrator monkey making the correct response (Fig. 2, top panel). Image identity and response location were confounded to maximize the chances of monkeys learning something from the demonstrator video. These videos thus allowed the monkeys to follow the demonstrator's response by imitative copying, stimulus enhancement, or location enhancement (Whiten et al. 2004). Trials were presented in a pseudo-random sequence, counterbalanced in blocks of 10 trials with 5 correct responses on the right, and with two trials without a video in each block. Each 260-trial session consisted of a single presentation of each of the 260 discrimination problems created using the 520 images described above. Monkeys were trained until they were at least 80% correct in a single 260-trial session. Throughout this manuscript, we use "session" to denote a set number of trials regardless of whether they were completed on the same day. In Experiment 1, each session was a single administration of each of the 260 image pairs.

Discriminations were image-location compounds. For a given image pair, the correct response was always to the same image and location. For example: if image A was the correct response and presented on the right on the first administration, that image would always be the correct response and presented on the right in each subsequent trial. The layout of test stimuli always matched what was demonstrated. In trials preceded by a video, monkeys could, therefore, solve each discrimination by either remembering the correct response from earlier sessions or by learning the choice of image or location demonstrated.

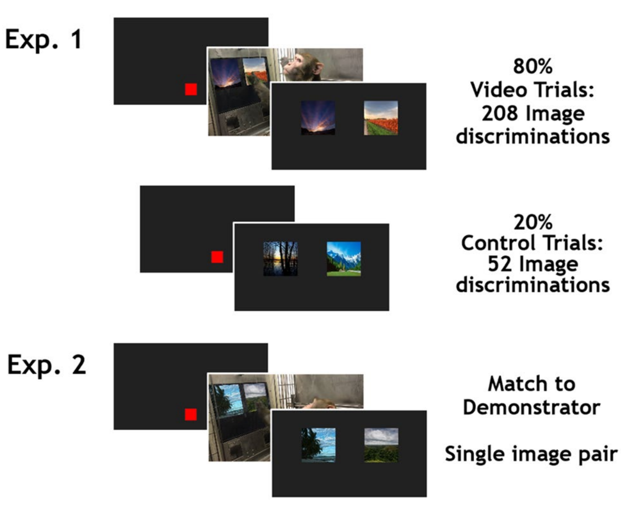

Fig. 2 Procedure for Experiments 1 & 2. Trials began with a red square that monkeys touched twice to start a trial. In Experiment 1, 80% of tests were preceded by a video showing the demonstrator monkey choosing between two images and retrieving a food reward. Twenty percent of the discriminations were never preceded by a video and could only be learned by trial and error. In Experiment 2, all trials were preceded by a video, and the same image pair was used throughout the experiment, with the correct image and response location counterbalanced. Thus, monkeys could not learn the discrimination by trial and error but instead had to make the same choice demonstrated in the video, trial by trial, to obtain a reward

Results & discussion

Videos did not facilitate learning of the discriminations (mean sessions to criterion on the subset of trials in each session with video = 10.66, without video = 10.83; paired-samples *t*-test: $t(5) = 0.237$, $p = 0.822$). We evaluated the number of sessions to criterion for each condition in Experiment 1 to assess the learning rate with a single within-subjects analysis, as each monkey needed a different number of sessions to reach the criterion on control and video trials. All 6 monkeys reached the criterion of one session at or above 80% correct. Monkeys improved their accuracy over the course of the first 10 sessions collapsed across conditions (Greenhouse–Geisser $F(1.467,7.333) = 24.066$, $p = 0.001$; Fig. 3; individual

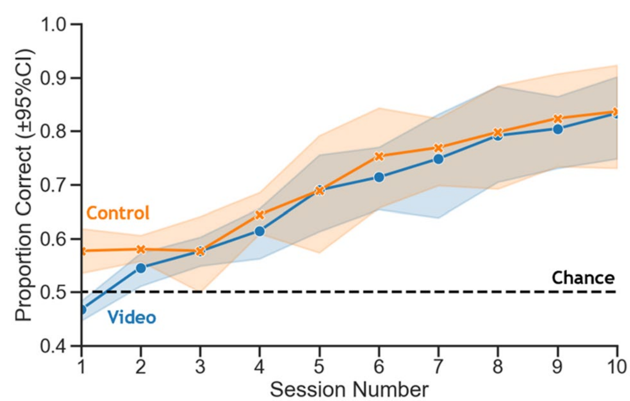

Fig. 3 Video demonstration did not accelerate learning or improve accuracy (blue circles), compared to control trials that could only be learned by trial and error (orange cross marks). Plotted are the first 10 sessions but some monkeys took more than 10 sessions to reach the criterion. Session number denotes a sequence of 260 trials regardless of whether they were completed on the same day. Each point on the video condition line comprises 208 trials per session, and each point on the control condition line comprises 52 trials per session. Shaded bands represent the 95% confidence interval around the mean. The dashed line is accuracy expected by chance

subject data from Experiment 1 are shown in Supp. Fig. 1 of Online Resource 1).

Monkeys did not spontaneously learn from the demonstrator in the videos and instead memorized the correct locations, the correct images, or both. These results suggest that monkeys do not readily learn from videos of conspecifics. However, evidence from chimpanzees suggests that they use social learning only when individual learning fails (Davis et al. 2016), and here individual learning was possible. In Experiment 2 we tested for social learning under circumstances that prevented individual learning.

Experiment 2: monkeys learned to use information in videos to guide choice when no other solution was available.

After finding in Experiment 1 that monkeys did not spontaneously learn from the behavior of the demonstrator monkey shown in videos, we designed Experiment 2 to test whether observer monkeys would use information in the demonstration video when doing so was the only way to perform above chance. Instead of training observer monkeys in concurrent discriminations that could be learned either by trial and error or using the video, Experiment 2 had only two images that were used for every trial and were different from any of the images shown in Experiment 1. The image shown as the correct choice in each video varied randomly from trial to trial. Repeating the same two images was a shift in task demand intended to make firsthand trial-and-error learning impossible. By making the correct response in each trial contingent on the choice made by the demonstrator in the video immediately preceding the subject monkeys' choices, we encouraged the observer monkeys to learn from the videos. If monkeys failed to learn from the demonstrator in Experiment 1 only because it was possible for observer monkeys to learn by trial and error, then they should learn from the demonstrator in this experiment where individual learning was not possible.

Procedure

We presented the monkeys with the same video templates from Experiment 1, but this time using a single pair of images (Fig. 2, lower panel). This task, therefore, resembled a match-to-sample paradigm where the videos acted as the sample, and the correct response was determined pseudorandomly from trial to trial.

We counterbalanced and pseudo-randomized which of the two images was the correct response and the location where it was displayed such that the only way to achieve performance above chance was to extract some information from the video preceding each trial. We used 4 video templates that showed the demonstrator selecting the image on the left, and 4 that showed the demonstrator selecting the image on the right. Each of these template videos was used to show image A on the left and image B on the right in one case, and the reverse in the other. These combinations yielded 8 videos of the demonstrator choosing image A and 8 videos of the demonstrator choosing B, counterbalanced for left–right location. Monkeys were administered at least 25 sessions of 160 trials, or until reaching criterion accuracy at or above 80% correct in a single session, whichever came later.

Results & Discussion

All 6 monkeys eventually learned to make the same choice as the monkey in the video on at least 80% of trials in a single 160-trial session (Number of sessions to criterion: $M = 25.67$ sessions, $SD = 14.62$, $max = 54$ sessions; individual subject data from Experiment 2 are shown in Supp. Fig. 2 of Online Resource 1). Accuracy improved significantly over the first 25 sessions (Fig. 4; Greenhouse–Geisser $F(2.350,11.750) = 7.990$, $p = 0.005$). The fact that monkeys achieved reliable high accuracy initially suggests that they learned from the demonstrator, but there were other features in the videos that the monkeys could associate with the correct response without learning from the demonstrator.

Because the images shown in the test were always in the same relative locations on the observer monkey's screen as they appeared in the demonstrator video, each video template reliably predicted the correct response location independently of the demonstrator's interaction with the task. For example, if video template A showed the demonstrator choosing the response on the left and ended with the

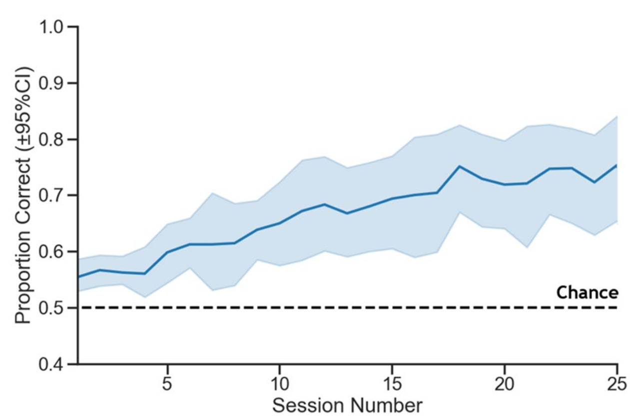

Fig. 4 Mean proportion responses matching the demonstrated choice in Experiment 2. Accuracy improved significantly with training, with all 6 monkeys eventually reaching the criterion. The solid line shows the mean proportion of trials correct across subjects. The shaded band represents the 95% confidence interval around the mean. The dashed line is accuracy expected by chance. Only the first 25 sessions are shown because that is the largest number of sessions all monkeys completed

demonstrator crouching, subjects could learn to choose the left image either by learning from the demonstrator or by memorizing that the left response is rewarded after the monkey crouches. As a result, learning which responses are occasioned by each video does not necessarily demonstrate that the monkeys learned from the demonstrator. We address this possibility in Experiment 3.

Experiment 3: tests with horizontally mirrored videos showed that monkeys learned something other than the demonstrator's responses

To test whether monkeys memorized idiosyncratic features of the videos and conditioned their responses on these, rather than learning from the demonstrator, we created horizontally mirrored versions of the videos used in Experiment 2 (Fig. 5). Mirroring the videos in this way meant that if the demonstrator monkey had selected the right image in the original video, it would now appear as if the demonstrator had selected the left image. If monkeys copied the demonstrator's choice in Experiment 2, then they should continue to select the image and location shown in the mirrored videos, even though this would be opposite to what the demonstrator selected when the video was first recorded. In contrast, if monkeys learned to respond to the left or right contingent upon features of the video that were not reversed by mirroring, then they should make the same choice whether the video was mirrored or not.

We also introduced probe trials to test whether the monkeys learned the response location or the identity of the image selected by the demonstrator in the video. On *response location* probes, subject monkeys chose between the same two locations as before, but grey squares replaced the images. If monkeys were responding based on location, they should continue performing above chance when image information was removed. On *image identity* probes, subject monkeys still chose between the two images shown in the demonstration video, but these were presented vertically so that neither occupied the locations shown in the demonstrator video. If monkeys responded based on image, rather than location, then they should continue to be more accurate than expected by chance in these trials.

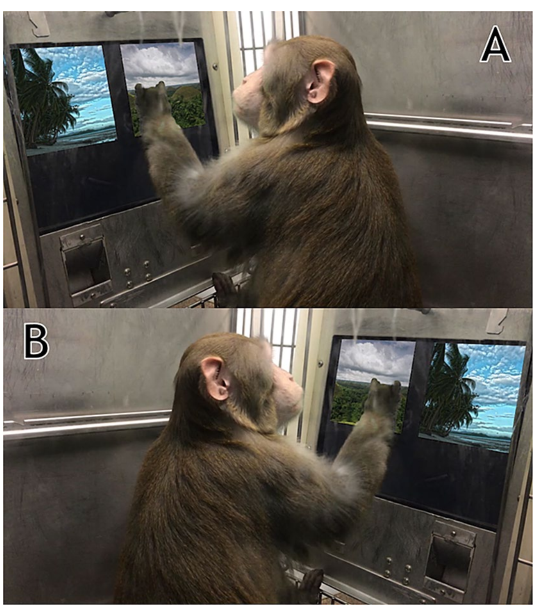

Fig. 5 Example of the horizontal mirroring used to create the new stimuli for Experiment 3. Panel A shows the original video in standard orientation. Panel B shows the same video after mirroring. Note that the images inlaid within each video are not mirrored, but the video around them is. This reverses the location that the demonstrator monkey appears to choose but maintains the identity of the chosen image, as well as other features of the video

Procedure

We first replicated the procedure from Experiment 2 until monkeys completed two consecutive 160-trial sessions at or above 85% correct to ensure that they regained proficiency on the task. After this initial training phase, the same videos were repeated in left–right-counterbalanced blocks of 8 trials with an additional ninth probe trial which was counterbalanced separately with the full set of all probe trials. This resulted in a total of 640 nine-trial blocks, or 5760 trials total. Probe trials were of five types depending on the combination of video mirroring and stimulus features available at test: response location, image identity, mirrored-video intact, mirrored-video image identity, or mirrored-video response location. On *intact* trials, the test stimuli reflected both the image identity and response location shown in the video. On *response location probes*, the test stimuli were presented in the original horizontal location from the video, but both images were replaced with grey squares. *On image identity probes*, the two choice images were presented vertically instead of horizontally, with the left image from the video being on top for half of the trials, and on the bottom for the other half. (Fig. 6).

Unmirrored intact training trials were only rewarded after a correct response to maintain proficiency on the task and comprised 88.9% of trials. All probe trials were rewarded regardless of the monkey's response, and each of the 5 probe types comprised 2.22% of trials (Fig. 6). On mirrored probe trials, the videos from each of the different trial types were mirrored horizontally (as shown in Fig. 5).

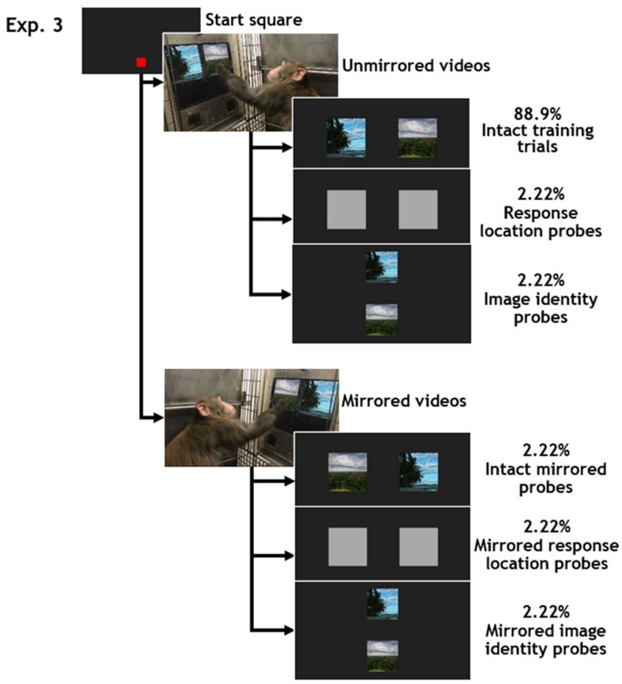

Fig. 6 Procedure for Experiment 3. Probe trials were always rewarded regardless of response; training trials were rewarded only for correct responses

Results & discussion

Monkeys did not learn from the behavior of the demonstrator monkey after the videos were mirrored. On probe trials with intact tests, they continued to respond to the locations the demonstrator had selected when the videos were initially created before they were mirrored. Thus, they copied the demonstrator significantly below chance on mirrored trials (Fig. 7, one-sample *t*-test with mirrored intact trials compared to chance: $t(5) = -3.754$, $p = 0.013$; individual subject data from Experiment 3 are shown in Supp. Fig. 3 of Online Resource 1). Observer monkeys maintained accuracy on unmirrored intact training trials (Fig. 7, one-sample *t*-test: $t(5) = 31.230$, $p < 0.001$). If monkeys had learned from the selections of the demonstrator, they would have reversed their choices following mirrored videos. They did not. It is unlikely that failure to learn from the demonstrator was caused by the novelty of the mirrored videos. If novelty impaired their ability to process the videos, they would have responded at chance. Instead, they gave the same response as the demonstrator significantly less frequently than expected by chance. This pattern of behavior indicates that whatever features of the videos conditioned responses to the left or right in the original videos remained and continued to control behavior after mirroring.

Under these conditions, we did not find evidence that the monkeys made selections based on the image or the location, either one. Monkeys did not perform differently from chance on either the *image identity* or *location* probe trials, regardless of whether the videos were mirrored (Fig. 7, unmirrored identity probes $t(5) = -0.675$, $p = 0.530$, mirrored $t(5) = 1.118$, $p = 0.314$; unmirrored location probes $t(5) = 2.276$, $p = 0.071$, mirrored $t(5) = 1.648$, $p = 0.160$). Obviously, monkeys had to use either location or image identity to guide their choice, but the probe trials used here may have been too disruptive to reveal this. It should be noted that the pattern of behavior on location probe trials is the same as seen with control trials, but not significant.

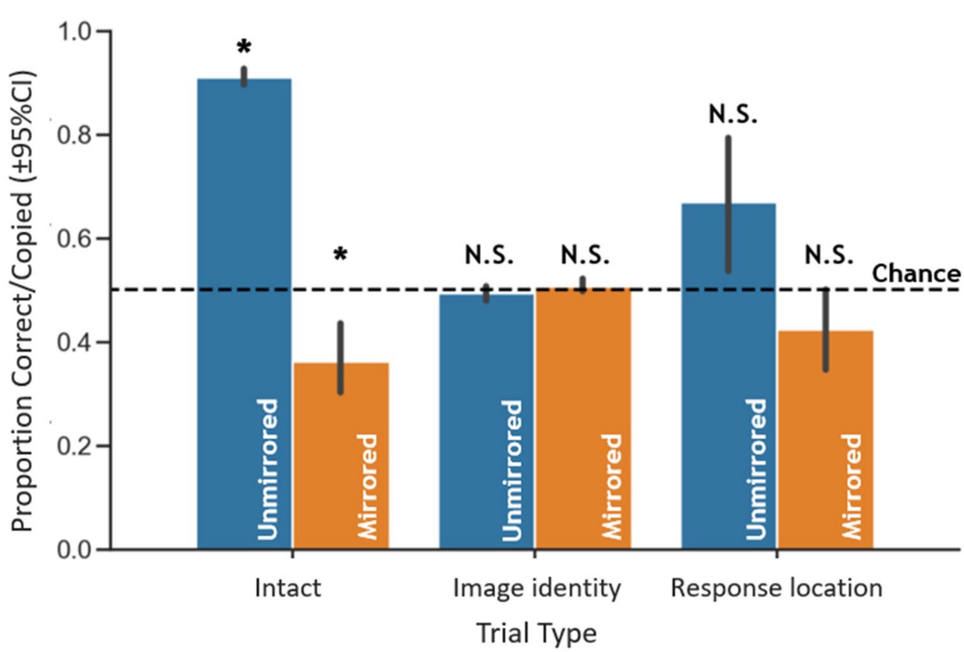

Fig. 7 Mean accuracy across different conditions in Experiment 3. Unmirrored intact trials were differentially reinforced, and comprised roughly 88.9% of trials, all other trial types were probe trials that were always reinforced regardless of subject response and comprised roughly 2.22% of the data each. Significance indicators (* for significant, N.S. for non-significant) refer to a one-sample *t*-test with $\alpha = 0.05$ on arcsine-transformed proportion correct values against chance performance (0.5 correct) performed separately for each trial type. Error bars represent the 95% confidence interval around each mean. The dashed line indicates chance

On location probe trials, several monkeys showed the same response pattern to location probe trials as they did to the intact trials, while others appeared to perform at chance on location probe trials regardless of whether the video was mirrored (Supp. Fig. 3 of Online Resource 1). It is possible that these probe trials were so distinct from regular trials that some monkeys treated them as an entirely new type of trial and as a result did not use any information from the demonstration video. This is made more likely by the fact that these trials were reinforced regardless of the response made at the test. We address this possibility for each probe type by introducing differential reinforcement in Experiments 4 and 5.

It seems likely that the relatively small number of video templates used in these experiments encouraged the use of arbitrary features to condition responding to the left or right. It is, therefore, still possible that the subjects would learn from the demonstrator if they were presented with differentially reinforced image-identity trials instead because the correct response on those could only be predicted by following the demonstrator's choice. We address this possibility in Experiment 4.

Experiment 4: monkeys did not learn the image choice of a demonstrator even after reinforced training

To further evaluate whether monkeys would learn from the behavior of a video demonstrator under conditions that strongly supported learning from the demonstrator's choices, we presented the monkeys with increasingly encouraging opportunities. In this set of experiments, we ensured that the only useful information in videos was the image selected by the demonstrator monkey. The location of the correct response was counterbalanced along the vertical axis, so monkeys could not learn an association between a video template and the direction in which to respond. If monkeys failed to learn from the demonstrator's choice of image only because they could instead learn to respond in a particular direction indicated by other cues in the videos, then they should learn the choice of images made by demonstrators once this spatial confound is removed.

Procedure

In Experiment 4A, we repeated the image identity trials from Experiment 3 but rewarded monkeys only if they selected the image selected by the demonstrator. Experiment 4B was identical to 4A, with the addition of a correction procedure to the protocol. If the observer monkey chose incorrectly, the same video and test trial were repeated until the monkey produced the correct response. In Experiment 4C, the procedure was identical to Experiment 4B, but the images used were high-contrast colorblind-visible patterns (Fig. 8, Exp. 4C). These stimuli were chosen to rule out the possibility that the monkeys were unable to learn from the demonstrator because the images used in the previous experiments were insufficiently visible or discriminable. For each of the three experiments, monkeys were presented with 25 sessions of 160 trials, equaling 12,000 training trials across the three experiments.

Results & discussion

Monkeys did not learn to choose the image selected by the demonstrator after image-identity trials were differentially reinforced (Fig. 9; Experiment 4A Greenhouse–Geisser $F(3.841, 19.207) = 1.196$, $p = 0.343$; individual subject data from Experiment 4 are shown in Supp. Fig. 4 of Online Resource 1). This remained the case even after a correction procedure was introduced in Experiment 4B (Fig. 9, Exp. 4B; Greenhouse–Geisser $F(4.350,21.751) = 1.117$, $p = 0.376$), and high-contrast stimuli were introduced in Experiment 4C (Fig. 9, Exp. 4C; Greenhouse–Geisser $F(3.675,18.376) = 1.620$, $p = 0.214$). Even though the correction procedure rapidly lowered the number of perseverative errors over the 25 sessions in Experiment 4B (Greenhouse–Geisser $F(1.547,7.734) = 12.033$, $p = 0.006$; Fig. 10), the subjects were unable to lean from the demonstrator's image choice in the video more than would be predicted by chance. It is, therefore, unlikely that monkeys performed at chance on image-identity probes in Experiments 3 and 4 only due to those trials being always reinforced.

In previous experiments, monkeys could have potentially relied on memorizing a response location for each

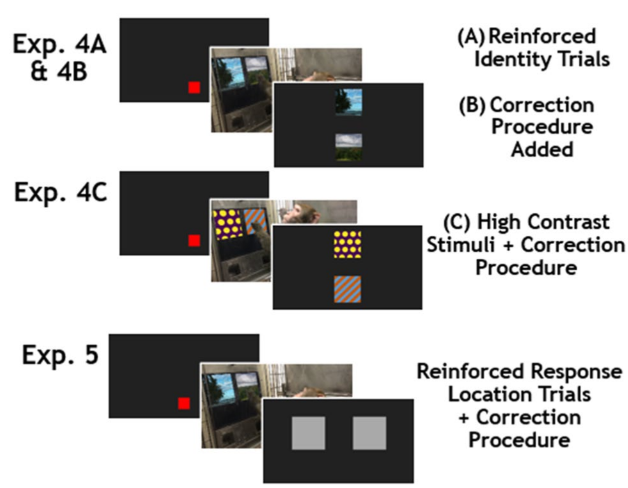

Fig. 8 Procedures for Experiments 4 & 5. Only correct choices were rewarded. The correction procedure added in Experiments 4B, 4C, and 5 was such that completing a trial incorrectly replayed the same video and repeated that trial until the monkey produced the correct response

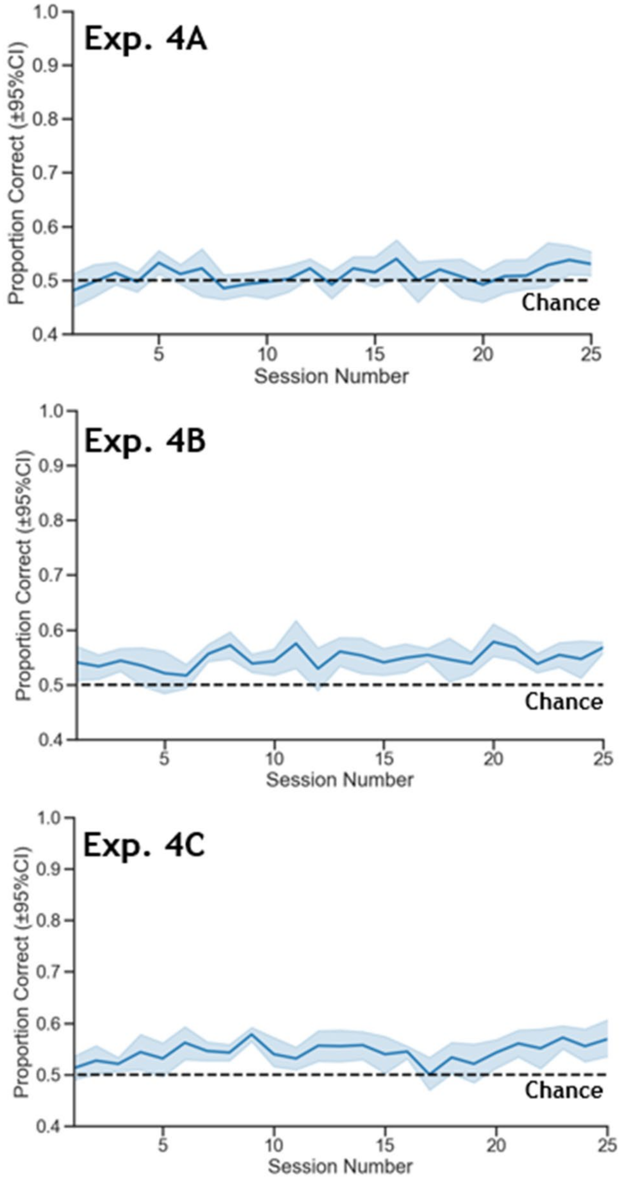

Fig. 9 Accuracy in Experiments 4A–4C. Subjects did not improve with training on the original task (Exp. 4A), after the introduction of a correction procedure (Exp. 4B), or after using high-contrast stimuli (Exp. 4C). The solid lines represent the mean proportion of correct trials on each experiment. The shaded bands represent the 95% confidence interval around the mean. Dashed lines represent expected performance at the chance level

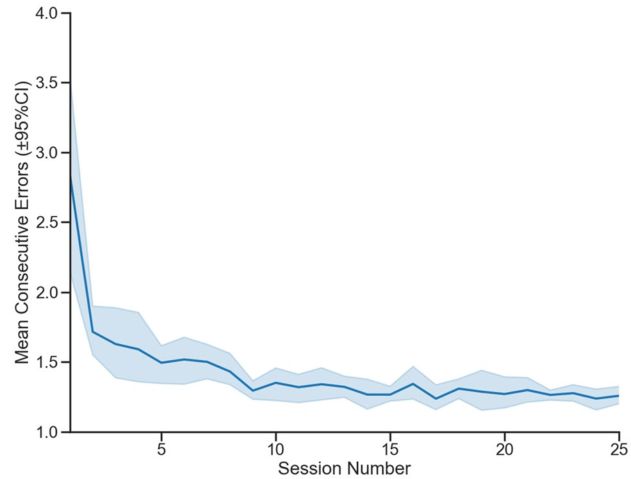

Fig. 10 Mean number of perseverative errors on incorrect trials before completing the trial successfully in Experiment 4B. The dramatic drop within the first few sessions indicates that the correction procedure did eliminate perseverative errors quite quickly. Solid line represents the mean number of consecutive errors on incorrect trials within a session. The shaded band represents the 95% confidence interval around that mean

video template, ignoring the specific images shown in each video. To test whether the subjects could overcome their prior memorization and make their choices based on the particular image selected by the demonstrator monkey, we trained them for 12,000 trials in which the image selected by the demonstrator was the only predictor of the correct response. They did not learn to identify the image touched by the demonstrator during all this training, despite the fact that these same monkeys readily responded on the basis of stimulus identity across a wide range of tasks (e.g., Templer et al. 2018; Lazareva et al. 2020; Brown and Hampton 2020), and learned to reverse response patterns in only a few trials (Hassett and Hampton 2017).

Across 12,000 trials for each monkey in Experiments 4A, 4B, and 4C, our monkeys failed to show any evidence of learning from the demonstrator's image choice in the videos, even after the introduction of a correction procedure and high-contrast images. Our monkeys, therefore, did not show any evidence of learning the demonstrator's image choice even after significant training.

Experiment 5: monkeys chose the location depicted in demonstrator videos

In Experiment 3, monkeys associated idiosyncratic features in each video with the correct response location, but only when both image identity and location were intact at the test. To address whether non-differential reinforcement was the reason they did not reliably follow the location association on probe trials, we tested whether the monkeys learned a response location association in the absence of image identity when they were only rewarded on correct trials. If our conclusion from Experiment 3 that the monkeys were associating some idiosyncratic feature of the video with a location response is correct, subjects should be able to rely on that association to improve their performance on trials where the responses presented at the test are identical except for their location on the screen.

Procedure

In Experiment 5, we repeated the location probes from Experiment 3, but monkeys were now only rewarded for correct responses (Fig. 8, Exp. 5). Monkeys were presented with at least seven sessions of 160 trials, or until they reached two consecutive sessions at or above 85% correct, whichever came later.

Subjects could still perform well in this task without learning from the demonstrator. Because each video template still depicted the same response location every time it was presented, the associations that monkeys previously learned between each video template and response location could be used on this task. If the monkeys learned to perform better than chance on intact trials in Experiment 3 by forming an association with response location, which is the only feature reliably predicted by video templates, then they will learn to choose the correct response location even when the image identities are no longer presented at test.

Results & discussion

Subjects quickly learned the correct response location on differentially reinforced location trials. All monkeys reached criterion within 24 sessions in this task (mean sessions to criterion = 11.5, SD = 7.47, max = 24 sessions), and showed significant learning over the first 7 sessions (Fig. 11, Greenhouse–Geisser $F(2.867,14.335) = 12.725$, $p < 0.001$; individual subject data from Experiment 5 are shown in Supp. Fig. 5 of Online Resource 1). Importantly, monkeys could still perform accurately on this task by relying on their previously learned associations between each video and the correct response location, and without learning from the demonstrator's behavior, as demonstrated by the mirrored videos in Experiment 3, so it is not likely that they quickly learned the correct response location on these trials using a new strategy different to the one they used to perform accurately on the intact trials in Experiment 3.

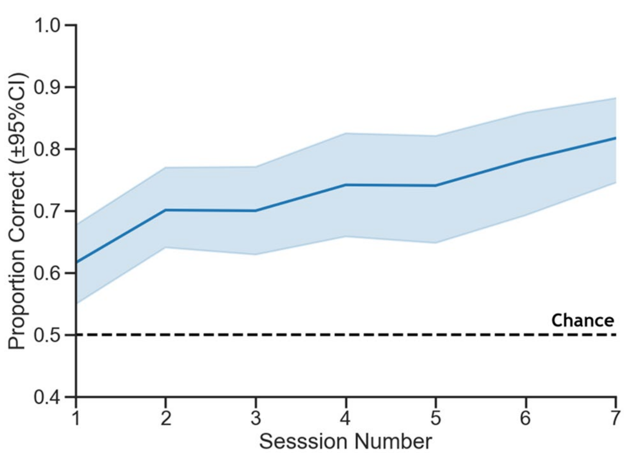

Fig. 11 Performance results on location trials from Experiment 5 for the first 7 sessions, which was the minimum number of sessions completed. All subjects reached the criterion of the task within 24 sessions. Solid line represents the mean proportion of trials completed correctly on the first attempt (i.e., not as part of the correction procedure). Shaded band represents the 95% confidence interval around that mean. Dashed line represents expected performance at the chance level

These results suggest that their near-chance accuracy on location-only probe trials in Experiment 3 may have been due to the non-differential reinforcement rather than a genuine inability to learn location responses separately from image identity. Combined with the results from mirrored-video trials in Experiment 3, it is likely that the monkeys had learned to associate some feature of each video with a particular response location whenever they relied on the videos to perform above chance in Experiments 2 and 3.

Experiment 6: a replication of probe trials with horizontally mirrored videos

Our conclusion that the monkeys learned to improve their accuracy on the task by associating idiosyncratic features of the videos with response location relies on the outcome of the horizontally mirrored intact probe trials in Experiment 3. In those trials, the monkeys did not change which location they selected for the test to match the new videos and instead continued to respond to the location previously associated with the videos before mirroring. To confirm the finding from those trials, we repeated the procedure of training the monkeys to criterion on the videos in their original orientation, then presented them with twice as many additional probe trials with horizontally mirrored videos identical to those presented in Experiment 3.

Procedure

As previously, the procedure from Experiment 2 was first replicated for each monkey until they completed two consecutive 160-trial sessions at or above 85% correct to ensure that they regained proficiency on the task. After this initial training phase, one in every eight out of 2048 trials was replaced with a probe trial in which the monkeys were presented with the same horizontally mirrored videos described in Experiment 3 followed by the two images presented in the same orientation as in the mirrored video (as shown in Fig. 6, intact mirrored probes). Probe trials were always rewarded regardless of subject response. This resulted in 256 mirrored probe trials per monkey.

Results & discussion

In this replication, as in Experiment 3, we did not find evidence that monkeys copied the actions of the demonstrator. Instead, they reliably responded to the same location whether the video was mirrored or not (Fig. 12, mirrored probes, one-sample *t*-test against choosing at random: $t(5) = -2.817$, $p = 0.019$). Meanwhile, subjects maintained accuracy on unmirrored training trials (Fig. 12, training trials, one-sample *t*-test: $t(5) = 13.755$, $p < 0.001$; individual subject data from Experiment 6 are shown in Supp. Fig. 6 of Online Resource 1). This replication corroborates our previous interpretation that monkeys were not performing better than chance on the training trials by learning from the demonstrator monkey, but rather by learning an arbitrary association between each video and a response location.

General discussion

Six adult male singly housed rhesus monkeys did not learn from the choices of a demonstrator shown in the video, even after extended training and various efforts to

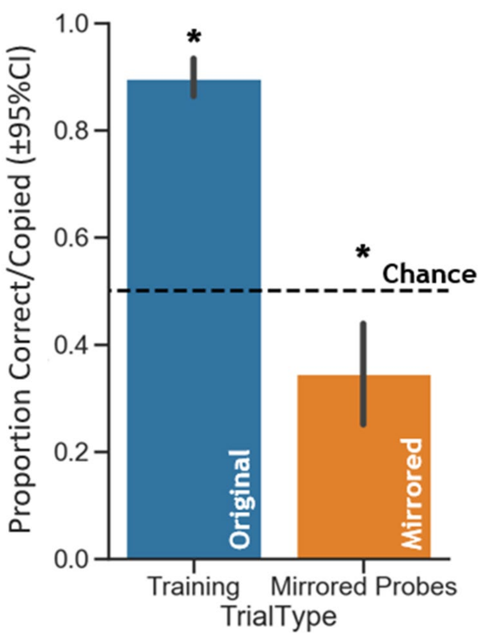

Fig. 12 Accuracy on training trials and horizontally mirrored probe trials. Unmirrored training trials were differentially reinforced and comprised 7/8ths of trials. Mirrored probe trials were always reinforced regardless of subject response and comprised the remaining 1/8th of trials. Significance indicators (* for significant) refer to a one-sample *t*-test with $\alpha = 0.05$ on arcsine-transformed proportion correct values against chance performance (0.5 correct) performed separately for each trial type. Error bars represent the 95% confidence interval around each mean. The dashed line represents expected chance performance at 0.5 correct

facilitate learning. While monkeys did learn to condition their left–right responses on the videos, our experiments with mirror image videos indicate that the features of the videos controlling the behavior of our monkeys were not impacted by the mirroring. If subjects had learned from the demonstrator's choices, they would have mirrored their responses along with the videos.

The experiments presented in this manuscript tested whether monkeys would use any of several social learning processes to facilitate learning. Given that we found no evidence of social learning with our paradigm, there is no target behavior to explain with a given social learning mechanism. Nonetheless, it is important to be clear about which social learning mechanisms could have potentially operated in our testing conditions, to evaluate the extent to which our paradigm allowed for the possibility of social learning. Following the taxonomy of social learning processes proposed by Whiten et al. (2004), one possibility was that monkeys would learn from the demonstrator by imitating his behavior directly. *Imitation* was possible in all the experiments presented here. In Experiment 1, because each video was repeated with each full cycle of the discrimination pairs, monkeys could also learn the discriminations preceded by videos faster through *observational conditioning* if they learned about the properties of the stimuli vicariously through the video as well as through their firsthand experience. In Experiments 2–6, monkeys could have learned to pay increased attention either to what or where the demonstrator was responding, and, therefore, learn by *stimulus or location enhancement,* respectively. After the videos were mirrored in Experiments 2 and 6, however, the monkeys neither chose the same image selected by the monkey nor changed their response location to match that of the mirrored demonstrator, suggesting that they did not benefit from either form of enhancement. Taken together, these results suggest that our paradigm did not engage imitation, observational conditioning, stimulus or location enhancement, or any other social learning mechanism in the six, adult, male, singly housed monkeys we tested in this study. This, of course, does not mean that rhesus monkeys, in general, lack these social learning mechanisms. These monkeys may be atypical due to their life in the laboratory, and our procedure using video demonstrations may have lacked critical features that support social learning in other contexts.

These findings differ from those reported by Meunier et al. (2007), in which rhesus monkeys benefitted from live conspecific demonstrations on a two-choice discrimination task. Rhesus monkeys may be able to learn socially from live conspecific demonstrations, but not from videos of such demonstrations, although Gunhold et al. report successful learning from video demonstrations in marmosets (Gunhold et al. 2014). Another potentially important difference between the Meunier et al. experiments and these experiments is that the rewarded item in each discrimination pair was held constant throughout their experiment, whereas our image-identity probe trials counterbalanced the rewarded stimulus, which required our monkeys to learn to follow the demonstrator's choice on each trial rather than vicariously learning a positive association with the rewarded stimulus through repeated second-hand presentations. In our first experiment, where discrimination pairs *were* held constant throughout the experiment, our monkeys did not benefit from the demonstrator videos. They learned the discriminations at the same rate whether the discriminations were preceded by a video or could only be learned by firsthand trial and error. Additionally, we tested the monkeys immediately following each demonstration, whereas Meunier et al. allowed their monkeys to observe a list of pairs being trained to criterion with a conspecific before their first test on that pair. Our monkeys might have benefited more from observing many demonstrations of each associative pairing without needing to follow an explicit rule of learning from the demonstrator behavior, although this account would contradict the cognitive imitation on a serial position learning task reported by Subiaul et al. (2004). In a previous experiment, rhesus monkeys readily solved a match-to-sample task where the correct response was shown among several distractors and indicated by a flashing border at training (Brady and Hampton 2018). When the images were shown again after a delay and without a border, monkeys were able to identify the image that had been cued in the study. This demonstration that a visual cue can guide monkeys' choice of the image at test, makes it all the more surprising that monkeys did not learn from the behavior of a demonstrator, which one would presume might be at least equally salient with a white border. The video demonstrations used in this study may not have provided a sufficiently salient signal of the correct response in each trial, or other information in the videos may have been distracting and, therefore, counter-effective in comparison to simply highlighting the correct response. The amount of information presented in each video may also be relevant to consider in future studies. It's possible that the videos we presented in this study contained too much information for the monkeys to parse for the relevant interaction within a six-second video clip. Given the number of training trials we allowed each monkey to learn from the demonstrator, however, it is unlikely that they would not have been able to habituate to any distractions in the videos and extract the relevant information.

It has been suggested that social learning in non-human primates may only occur when the underlying task is difficult enough to render individual learning unlikely or very difficult (Whiten et al. 2009). Chimpanzees have been shown not to switch from individual foraging strategies to more efficient socially learned ones unless their individual strategies become ineffective (Davis et al. 2016). If there is a threshold of task difficulty or baseline reward rate below which monkeys are not willing to learn from conspecifics, it is possible that the task used in our experiments was not challenging or novel enough to warrant engaging in social learning. We addressed this possibility in Experiment 4, on which monkeys could only perform better than chance by learning the identity of the image the demonstrator chose and not by attending to some irrelevant feature of the video. Despite the introduction of the correction procedure, which lowered perseverative errors substantially, this did not result in monkeys learning from the demonstrator. Nevertheless, having only two possible responses on a given trial—which we chose to keep the images relatively large on the computer screen in the video demonstrations—may have produced a sufficient reward rate when performing at chance such that monkeys did not find the task sufficiently challenging to recruit social learning.

In our experiments, the monkeys only had the opportunity to learn from observing correct responses, because the videos always showed the demonstrator monkey completing the trial successfully and obtaining a food reward. Some previous work has suggested that monkeys learn more from observing errors compared to successes (Monfardini et al. 2014; Isbaine et al. 2015). It is possible that the lack of errors by the demonstrator slowed learning in our experiments, but it is unlikely that the lack of incorrect trials would have prevented our monkeys from learning entirely.

Although monkeys appear to gather social information from videos or images in some circumstances (e.g., Parr et al. 2000; Bovet and Washburn 2003; Paxton et al. 2010; Gunhold et al. 2014), it is possible that the monkeys in our study did not experience the videos as social at all. Even when our monkeys learned to attend to *something* in each video, they did not learn from the behavior of the demonstrator. This lack of social facilitation would not entirely account for the monkeys' inability to learn the image-identity trials in Experiment 4, however, since they are capable of similar learning in asocial match-to-sample tasks. Since monkeys are capable of learning to remember images highlighted with a border in the absence of any social facilitation, the fact that they do not learn to identify the image that is covered by the demonstrator's hand suggests that they were less proficient at this task than would be predicted simply by the absence of social facilitation. More generally, studies with chimpanzees, orangutans, and capuchin monkeys show that all these species benefit from two-dimensional videos to guide their navigation in a three-dimensional environment (Poss and Rochat 2003; Leighty et al. 2008; Potì and Saporiti 2010). Rhesus macaques are also very similar to humans in their color-vision and flicker fusion (D'Eath 2007), so video displays designed for human vision should work reasonably well for the monkeys in our experiments. Some previous studies have reported that monkeys can learn in some contexts from humans or ghost displays (e.g., Isbaine et al. 2015; Ferrucci et al. 2019; Nougaret et al. 2019), while others found no learning from a human demonstrator or an animated arm (Anderson et al. 2017; Renner et al. 2021). One study also found that monkeys learn better from a human imitating a monkey model than a human behaving normally and concluded that model-observer similarity is important for observational learning (Monfardini et al. 2014). Given that a conspecific performing the same task is the closest facsimile possible to a real-life demonstration, and that monkeys learn from videos in other contexts, it is surprising that our monkeys did not learn from the demonstrator in the videos we used. Rhesus monkeys have also been shown to acquire fear of toy snakes by watching videos of conspecifics reacting to them fearfully (Cook and Mineka 1990). In the same study, those monkeys did not acquire a fear response to artificial flowers when the videos were edited to show artificial flowers instead. This contrast with our findings suggests that rhesus monkeys may learn strong emotional responses from videos more readily than they do other behavioral responses.

The demonstrator monkey filmed in these videos was one of the six monkeys tested in this study. He is identified as monkey "G" in Supp. Figs. 1–7 of Online Resource 1. During filming, this monkey was only shown solid green squares as response options, as shown in Fig. 1, top-left panel. Like the other five monkeys, monkey "G" did not see the images that were later added to the videos until the start of testing. Although monkeys have been reported to extract information about social interactions from videos, it is relatively harder for them to extract the identity of specific individuals from those videos (Paxton et al. 2010; but see Pokorny and de Waal 2009). And while evidence from the mirror self-recognition test with monkeys has been debated in the literature (e.g., Chang et al. 2015; Anderson and Gallup 2015), even studies where monkeys do show mirror self-recognition require substantial experience and/or training with mirrors before monkeys recognize themselves. Video footage would be even more difficult as a basis for self-recognition since the movements in the video do not correspond with the viewer's actions. It is, therefore, unlikely that the demonstrator monkey recognized himself in the edited videos he was presented as a learner in these experiments. In the present study, the monkey who was recorded to generate the video demonstrations was not an outlier in terms of accuracy on any of the tasks, suggesting that watching video demonstrations of himself did not significantly impact his performance compared to the other monkeys.

Finally, several species of non-human primates have been found to learn selectively from conspecifics depending on features of the demonstrator like age, dominance rank, sex, and familiarity (Kendal et al. 2018). It is possible that our subjects did not learn from the demonstrator because of their life history. Captive adult male rhesus monkeys may not learn from other adult male rhesus monkeys. Further work may be necessary to understand the effects of life history on the extent to which laboratory rhesus monkeys learn socially. If our findings are not unique to captive monkeys, or to our monkeys in particular, this possibility would suggest at least one significant limitation on the spread of behaviors within rhesus monkey groups: that transmission is less likely to occur between adult males.

The six adult male rhesus monkeys tested in this study did not learn two-choice discrimination problems from a conspecific's choices shown in videos. Under some conditions, they falsely appeared to learn from the demonstrator, but the mirror-reversal of the videos indicated that they did not rely on the demonstrator's behavior, but instead followed other cues in the videos. Even after significant training, and when individual trial-and-error learning was not possible, these monkeys did not match their response to the response made by the video demonstrator. To understand the learning mechanisms underlying the transmission of behaviors across individuals that has been reported in wild monkeys, controlled social learning experiments are necessary to test the specific elements of social interactions that facilitate learning. Rather than investigating whether monkeys can or cannot imitate as a dichotomy, greater insights into the evolution of primate social learning may be gained by systematically testing the specific limitations that prevent monkeys from learning by observation in some contexts but not others.

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Declarations

Conflict of interest The authors have no competing interests to declare.

Human and animal rights All procedures involving animals were approved by the Emory University Institutional Animal Care and Use Committee (IACUC). The datasets generated and/or analyzed during the current study are available from the corresponding author on reasonable request.

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