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Adult Rhesus Monkeys do not Copy the Choices of a Conspecific Shown in Videos

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B.S., Rider University, 2014

Advisor: Robert Hampton, Ph.D.

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A thesis submitted to the faculty of the
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Abstract

Adult Rhesus Monkeys do not Copy the Choices of a Conspecific Shown in Videos

By Jad Nasrini

Evidence of socially learned animal traditions has accumulated from mostly observational field studies. In contrast, laboratory experiments with monkeys often fail to find the social learning thought to be necessary for animal traditions to form in the wild. We investigated social learning by presenting Rhesus monkeys with videos of a conspecific solving two-choice discrimination tasks. With training, monkeys gradually learned to correctly follow videos of a demonstrator, however, follow-up experiments revealed that this accuracy improvement was not due to copying the behavior of 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, they did not exceed chance over 12,000 training trials. Because monkeys readily learn to follow nonsocial visual cues to guide image choice, their inability to copy a demonstrator here indicates substantial limitations in the capacity for social learning in monkeys. Furthermore, these findings encourage deeper consideration of what monkeys perceive when presented with video stimuli on computer screens.

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1. Introduction

Field evidence of animal traditions has accumulated across many taxa over the past few years (Whiten, 2021). Yet despite many examples of group-specific behaviors thought to be socially learned in wild monkeys, experimental studies have reported conflicting evidence on the extent to which monkeys learn novel behaviors by observation (Visalberghi & Fragaszy, 2002; Subiaul, 2007; Subiaul et al., 2016). Some authors have suggested that social learning is not a unitary behavior in monkeys and may be present in some contexts but not others (Subiaul et al., 2016). For instance, monkeys may socially 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 that is transmitted through observation.

In social learning experiments involving live demonstrations, it is difficult to control the types of information that a conspecific demonstrator provides the learner. Video-recorded demonstrations may offer experimental advantages because they allow the possibility of precisely controlling the information available to the learner to copy. While live demonstrations offer the closest analog to opportunities for social learning in the wild, previous work has shown that monkeys can learn some behaviors from videos (Gunhold et al. 2014) and can recognize and extract social information about conspecifics from videos (Adachi & Hampton, 2011; Mosher et al., 2011; Parr et al., 2000; Paxton et al., 2010; Pokorny & de Waal, 2009). It may also not be sufficient to investigate copying at a single time point to determine the extent of social learning capabilities within a species. The likelihood to engage in social learning may change over the course of an individual animal's life history (Heyes, 2012, 2016).

In this study, we tested the feasibility of using pre-recorded video demonstrations by a conspecific to investigate both the spontaneous likelihood for monkeys to engage in social learning from videos, as well as whether that likelihood changes after many training sessions in which monkeys are rewarded for following demonstrations.

We also used these video demonstrations to investigate whether monkeys learn the visual features, or the location of a rewarded stimulus as demonstrated by a conspecific. Finally, in cases where monkeys appeared to learn from the videos, we also tested whether they truly learned to copy the behavior of the demonstrator monkey or learned to associate some other feature of the videos with the correct response.

Because previous laboratory experiments have found mixed results when testing social learning in monkeys, we opted to investigate social learning under maximally permissive conditions: in a two-image choice task, where monkeys do not have to learn a new motor response and can perform accurately by copying either the stimulus or location that a demonstrator monkey interacts with to receive a food reward.

2. Subjects & Materials

2.1. 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 Yerkes National Primate Research Center were used. Monkeys were reared in natural family groups at the Yerkes 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 colony room, 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 were frequently given the opportunity to view a small set of 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 (Figure 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.

2.2. 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 (Figure 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 sound and a food pellet being dispensed to the demonstrator monkey. This procedure allowed us to demonstrate 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 seconds long.

Figure 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 correct discrimination choices.

2.3. Statistical Analyses

All analyses were conducted using SPSS version 27. In all cases where proportion scores were used in rANOVA or one-sample t-tests, the proportions were first arcsine-transformed using the formula (2*arcsine(sqrt(proportion)). Wherever rANOVA was used, the degrees of freedom were adjusted for sphericity violation using the Greenhouse-Geisser correction.

3. Experiment 1: Monkeys did not spontaneously copy 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 copying the behavior of the monkey in a video preceding each trial. 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.

3.1. Procedure

Monkeys were trained with 260 image discriminations concurrently. Eighty percent of these discriminations were always preceded by a video of the demonstrator monkey making the correct response, affording the possibility of copying the correct response. Twenty percent of the discriminations were never preceded by a video, requiring that monkeys learn by trial and error (Figure 2, top panel). Trials were presented in 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. Monkeys were trained until they were at least 80% correct in a single 260 trial session.

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 presentation of test stimuli always matched what was demonstrated for discriminations preceded by a video. On trials preceded by a video, monkeys could therefore solve each discrimination by either remembering the correct response from earlier sessions, or by copying the demonstrated image or location.

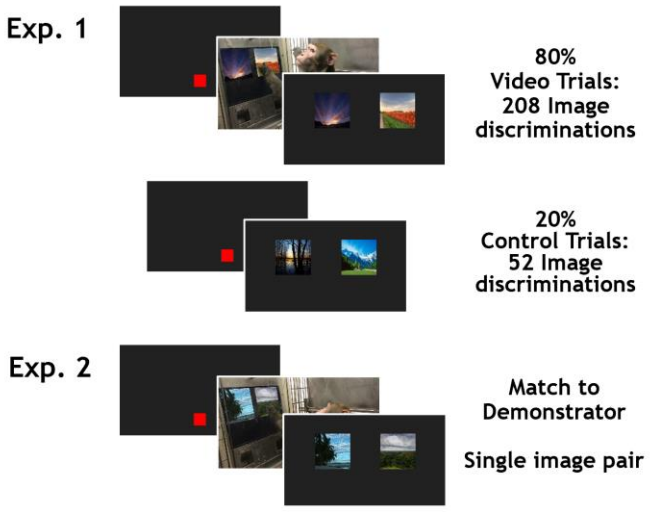

Figure 2. Procedure for Experiments 1 & 2. Monkeys were first presented with a red square they touched twice to start a trial. In Experiment 1, 80% of the discriminations were preceded by a video showing the demonstrator monkey choosing between two images and retrieving a food reward. Twenty percent 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 being counterbalanced, such that monkeys could not learn a set of discriminations by trial and error and had to attend to the videos to improve their accuracy.

3.2. Results & Discussion

Videos did not facilitate learning of the discriminations (mean sessions to criterion with video=10.66, without video=10.83; paired-samples t-test: $t(5)=0.237$, p=.822). All 6 monkeys reached the criterion of one session at or above 80% correct. Monkeys significantly improved their accuracy over the course of the first 10 sessions collapsed across condition (Greenhouse-Geisser $F(1.467,7.333)=24.066$, p=.001; Figure 3).

Monkeys did not spontaneously copy the demonstrator in the videos and instead memorized the correct locations or the correct images (or both). These results seem to indicate 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). In

Experiment 2 we tested for social learning under circumstances that prevented individual learning.

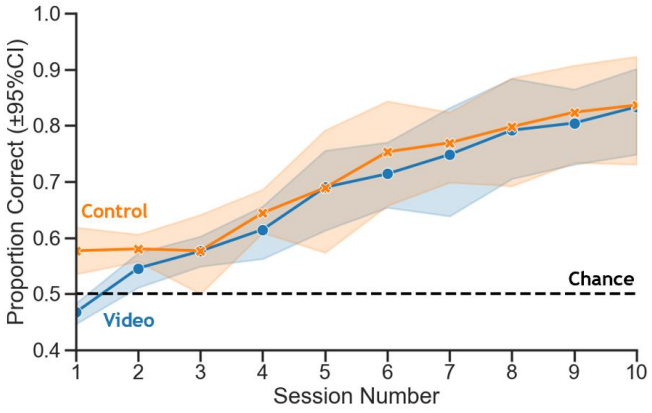

Figure 3. Learning occurred at a similar rate for discriminations preceded by a video (blue), and for control trials that could only be learned by trial and error (orange). Plotted are the first 10 sessions but some monkeys took more than 10 sessions to reach criterion. Shaded bands represent the 95% confidence interval around the mean. The dashed line is accuracy expected by chance.

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

After finding that monkeys did not spontaneously copy the behavior of the demonstrator monkey shown in videos, we designed Experiment 2 to test whether they would do so when that was the only way to perform consistently above chance. Instead of training the monkeys in concurrent discriminations that could be learned either by trial and error, or by copying the choice of the demonstrator, we required them to make the same choice the monkey in each sample video made, and these choices varied randomly from trial to trial. If monkeys failed to copy the demonstrator in Experiment 1 only because learning by trial and error was possible, then they should copy the demonstrator in this experiment.

4.1. Procedure

We presented the monkeys with the same video templates from Experiment 1, but this time using a single pair of images (Figure 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 pseudo-randomly 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 level 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. All monkeys were administered sessions until reaching criterion accuracy at or above 80% correct.

4.2. Results & Discussion

All 6 monkeys gradually learned to make the same choice as the monkey in the video (Figure 4). Accuracy improved significantly over the first 25 sessions (Greenhouse-Geisser $F(2.350,11.750)=7.990$, $p=.005$). All 6 monkeys reached the criterion of accuracy at or above 80% correct, but with large inter-subject variability in the number of sessions required to achieve this criterion (Number of sessions to criterion: M = 25.67 sessions, SD=14.62, max=69 sessions).

That fact that monkeys achieved reliable high accuracy suggests that they copied the demonstrator. However, the slow and steady rate at which performance improved across sessions is maybe more consistent with memorizing which videos cue which responses, rather than learning to follow the rule "copy the choice of the demonstrator."

Because the images shown at test were always in the same relative locations on the subject 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 shows the demonstrator choosing the response on the left and ends with the demonstrator crouching, subjects could learn to choose the left image either by copying the demonstrator or by memorizing that the left response is rewarded after the monkey crouches. As a result, learning the correct responses after each video does not necessarily demonstrate that the monkeys learned to copy from the demonstrator in this experiment. We address this possibility in Experiment 3.

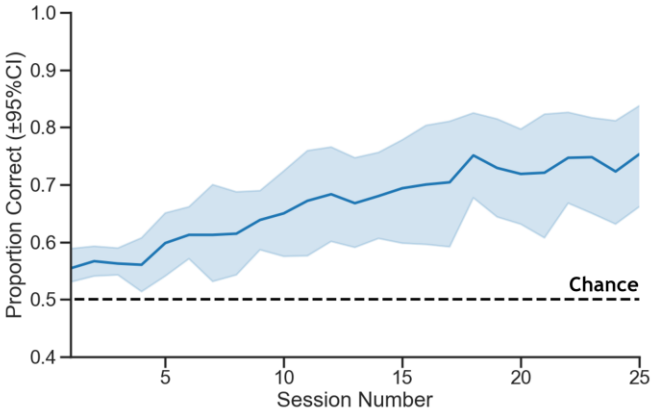

Figure 4. Mean proportion correct in Experiment 2. Accuracy improved significantly with training, with all 6 monkeys eventually reaching criterion. The solid line shows the mean proportion of trials correct across subjects. The shaded band represents the 95% confidence interval around the mean. The dashed line is accuracy expected by chance. Only the first 25 sessions are shown because one monkey achieved criterion in 25 sessions.

5. Experiment 3: Tests with horizontally mirrored videos showed that monkeys learned something other than "copy the demonstrator"

Although the monkeys learned to respond based on the video preceding each trial in Experiment 2, this does not prove that they were copying the demonstrator. Monkeys could achieve high accuracy by copying, but it is also possible for monkeys to learn to respond to other kinds of information in the videos. For example, monkeys may have learned to respond on the left whenever the demonstrator monkey moves his head in a particular way, or whenever a particular piece of the testing apparatus was covered for part of the video, or whenever a particular background sound played during the video.

To test whether monkeys memorized idiosyncratic features of the videos and conditioned their responses on these, rather than copying the behavior of the demonstrator, we created horizontally mirrored versions of the videos used in Experiment 2 (Figure 5). 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. Conversely, if monkeys learned to respond to the left or right contingent upon features of the video other than the demonstrator's choice, 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 two locations, but grey squares replace the images. On image identity probes, subject monkeys chose between two images presented vertically so that neither occupied the locations shown in the demonstrator video. If monkeys learned either the

correct response location or image identity they should choose after each video, then they should continue to perform above chance when the responses at test depict either the response location or the same images in the absence of the other feature of the stimuli in the videos.

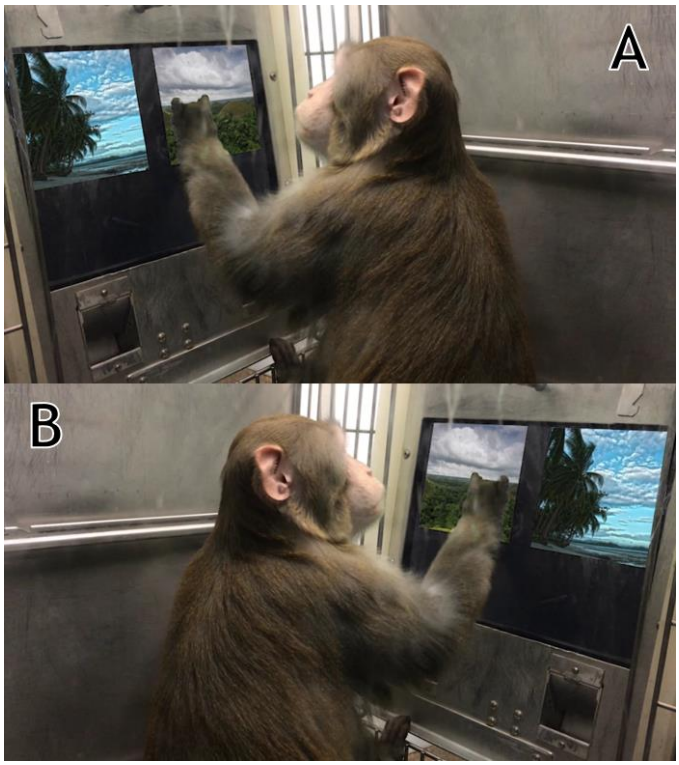

Figure 5. Example of the horizontal mirroring used to create the new stimuli for Experiment 3. Panel A shows the original video in standard orientation. Panel B shows the same video after mirroring. Note that the images inlaid within each video are not mirrored, but the video around them is. This reverses 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.

5.1. Procedure

We first replicated the procedure from Experiment 2 until monkeys completed two consecutive 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 administered, or 5,760 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 training and probe 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. (Figure 6).

Unmirrored intact training trials were only rewarded after a correct response to maintain proficiency on the task and comprised 88.9% or 5,120/5,760 of the trials collected. All probe trials were rewarded regardless of the monkey's response, and each of the 5 probe types comprised 2.22% or 128/5,760 of trials administered. (Figure 6). On mirrored probe trials, the videos from each of the different trial types were mirrored horizontally (as shown in Figure 5).

Mirroring the videos horizontally reversed which location the demonstrator chose in the video, while preserving many other features of the videos. In the example shown, video A would have been associated with reward for responses to the right. After mirroring, video B maintains all of the background features in video A, but the demonstrator is now shown choosing the left image. If subject monkeys copy the demonstrator, they should switch their response to the new location after mirrored probe trials (on the left for video B in the example below). If they instead maintained the original response (responding on the right for video B), that would suggest that they learned to associate an idiosyncratic feature of the video with responding on the right regardless of the demonstrator's behavior.

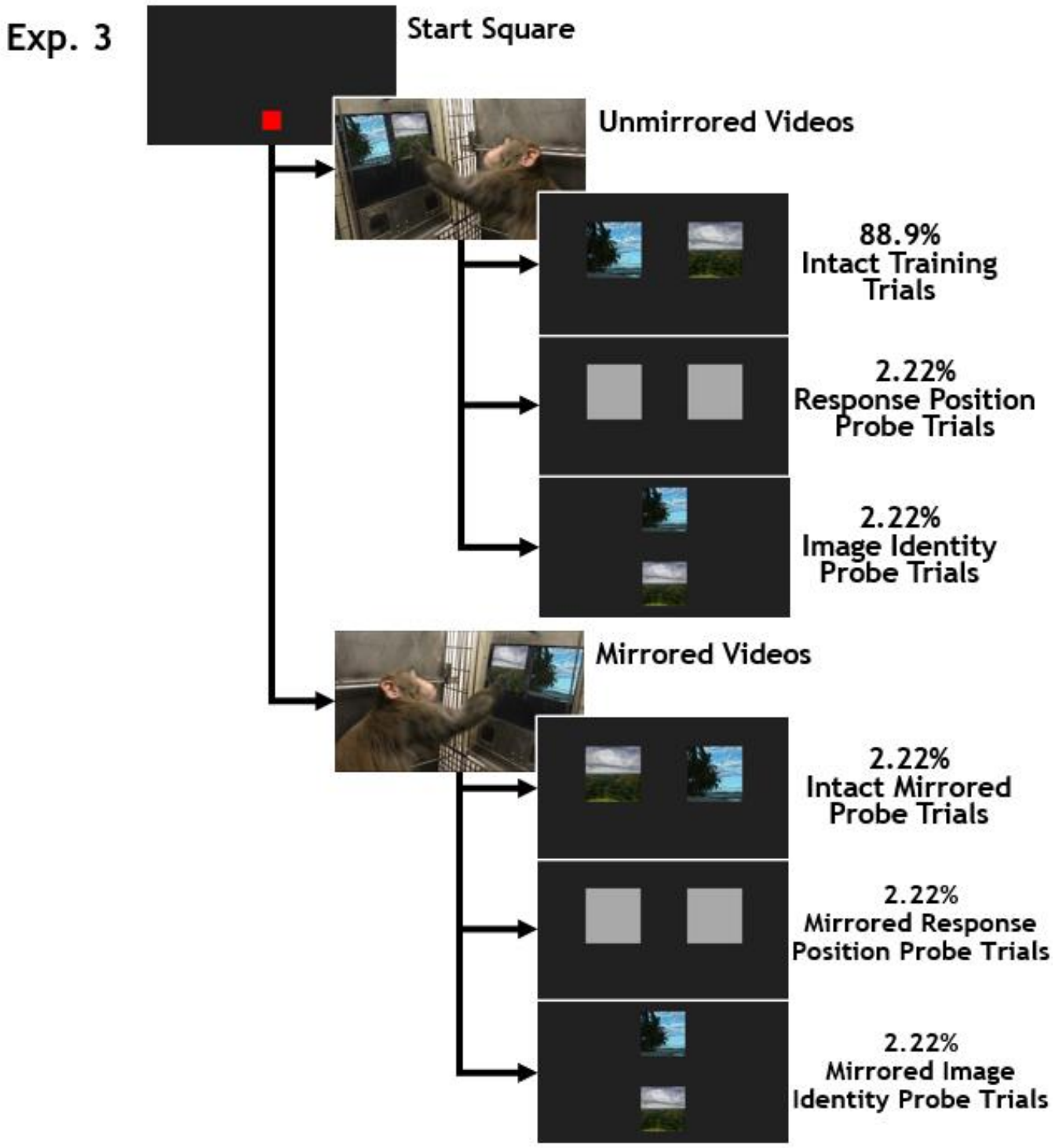

Figure 6. Procedure for Experiment 3. Probe trials were always rewarded regardless of response; training trials were rewarded only for correct responses.

5.2. Results & Discussion

Monkeys did not copy the behavior of the demonstrator monkey after the videos were mirrored. On probe trials with intact tests, they continued to respond to the location shown in the videos before they were mirrored (Figure 7, one-sample t-test with mirrored intact trials compared to chance: $t(5)=-3.754$, $p=.013$). subjects maintained accuracy on unmirrored intact training trials (Figure 7, one-sample t-test: $t(5)=31.230$, $p<.001$).

Monkeys did not perform differently from chance on either the identity or location probe trials, regardless of whether the videos were mirrored (Figure 7, unmirrored identity probes $t(5)=-0.675$, $p=.530$, mirrored $t(5)=1.118$, $p=.314$; unmirrored location probes $t(5)=2.276$, $p=.071$, mirrored $t(5)=1.648$, $p=.160$).

If monkeys copied the actions of the demonstrator, they should have reversed their choices following mirrored videos. They did not. It is unlikely that failure to copy was caused by the novelty of the mirrored videos. If novelty impaired their ability to process the videos, they would have responded at chance. Copying the demonstrator significantly less frequently than would be predicted by chance after the videos were horizontally mirrored indicates that whatever feature of the videos conditioned responses to the left or right remained present and evident to the monkeys after mirroring.

It is possible 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 to copy the demonstrator if they were presented with differentially reinforced image-identity trials instead. We address this possibility in Experiment 4.

Finally, because probe trials were non-differentially reinforced, and test trials for both probes were visually distinct from control trials, it's possible that the monkeys developed entirely new response strategies for these new probe types instead of generalizing from their training on intact trials. For example, monkeys might have learned the rule "choose the left response whenever two gray squares are presented", for which they would have always been reinforced. We address this possibility for each probe type by introducing differential reinforcement in Experiments 4 and 5.

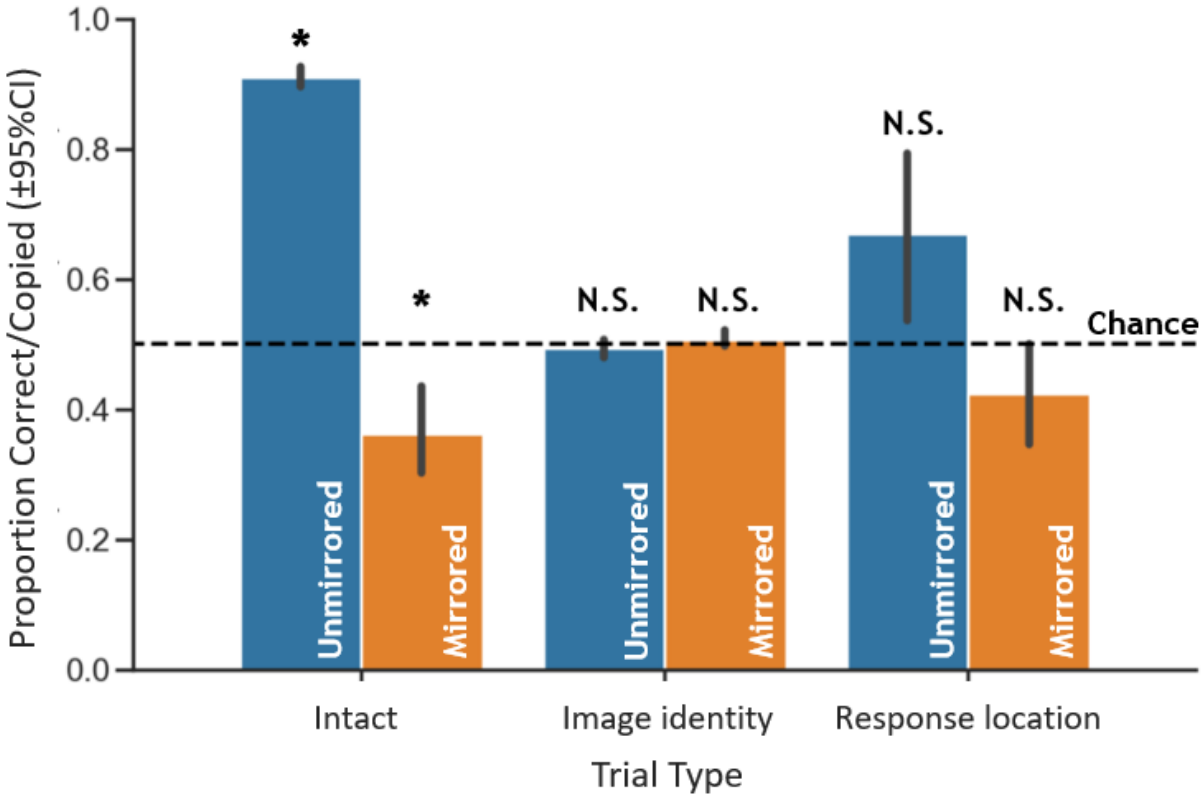

Figure 7. Mean accuracy across different conditions in Experiment 3. Unmirrored intact trials were differentially reinforced, and comprised roughly 88.9% of trials, all other trial types were probe trials that were always reinforced regardless of subject response and comprised roughly 2.22% of the data each. Significance indicators (* for significant, N.S. for non-significant) refer to a one-sample t-test with α=.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.

6. Experiment 4: Monkeys did not copy the image choice of a demonstrator even after training

To further evaluate whether monkeys would copy the behavior of a video demonstrator under any conditions we presented the monkeys with increasingly permissive opportunities. In this set of experiments, we ensured that the only useful information in videos was the image selected by the demonstrator monkeys. 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 did not match the demonstrator's choice of image only because they could instead learn to respond in the direction cued by the videos, then they should learn to copy the choice of image by demonstrators once this spatial confound is removed.

6.1. 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 subject monkey chose incorrectly, the same video and test trial 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 (Figure 8, Exp. 4C). These stimuli were chosen to rule out the possibility that the monkeys were unable to copy 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.

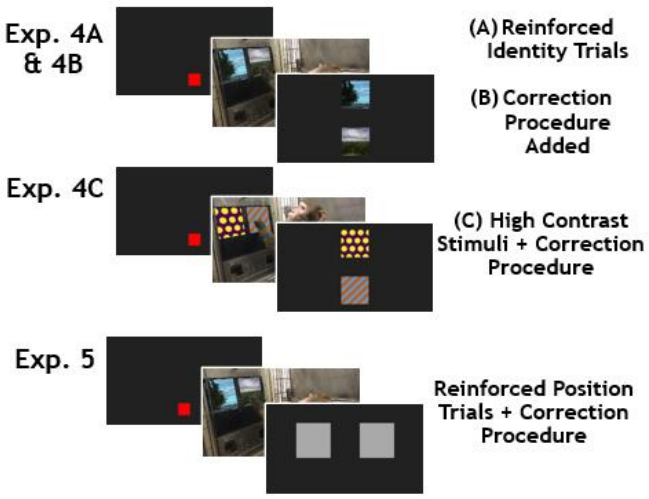

Figure 8. Procedures for Experiments 4 & 5. Only correct choices were rewarded. The correction procedure added in Experiments 4B, 4C, and 5 was such that completing a trial incorrectly replayed the same video and repeated that trial until the monkey produced the correct response.

6.2. Results & Discussion

Monkeys did not learn to choose the image selected by the demonstrator after image-identity trials were differentially reinforced (Figure 9; Experiment 4A Greenhouse-Geisser $F(3.841, 19.207) = 1.196$, $p=.343$). This remained the case even after a correction procedure was introduced in Experiment 4B (Figure 9, Exp. 4B; Greenhouse-Geisser $F(4.350,21.751)=1.117$, $p=.376$), and high-contrast stimuli were introduced in Experiment 4C (Figure 9, Exp. 4C; Greenhouse-Geisser $F(3.675,18.376)=1.620$, $p=.214$). Even though the correction procedure rapidly lowered the number of perseverative errors over the 25 sessions in Experiment 4B (Greenhouse-Geisser $F(1.547,7.734)=12.033$, $p=.006$; Figure 10), the subjects were unable to copy the demonstrator's image choice from 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.

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

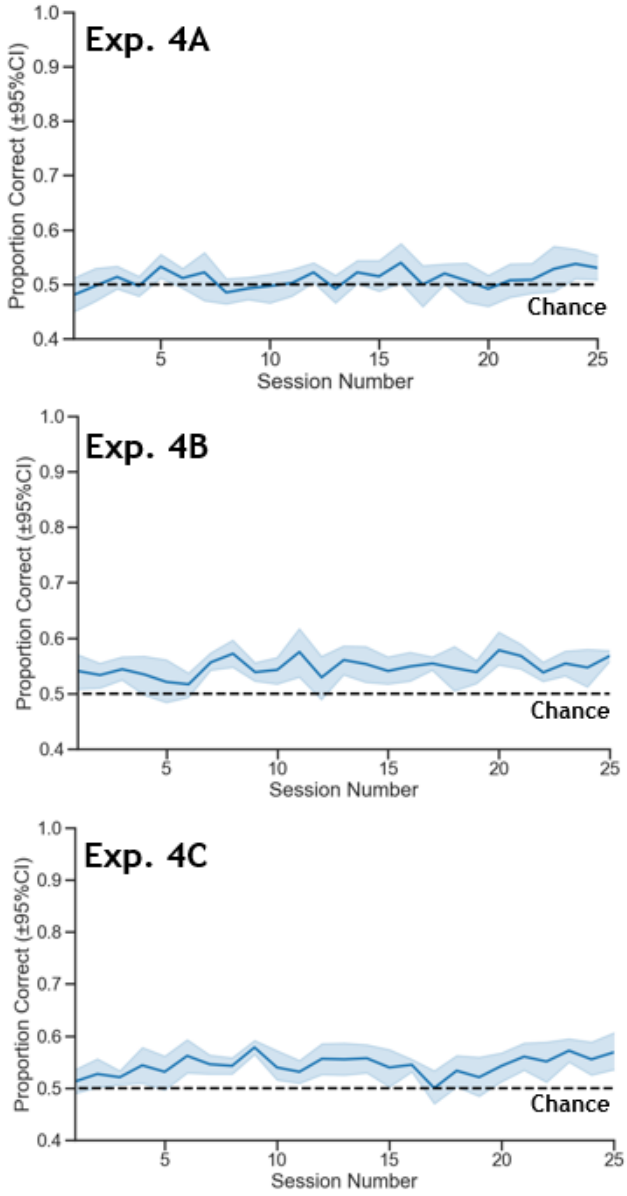

Figure 9. Accuracy in Experiments 4A-4C. Subjects did not improve with training on the original task (Exp. 4A), after the introduction of a correction procedure (Exp. 4B), or after using

high-contrast stimuli (Exp. 4C). The solid lines represent 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 chance level.

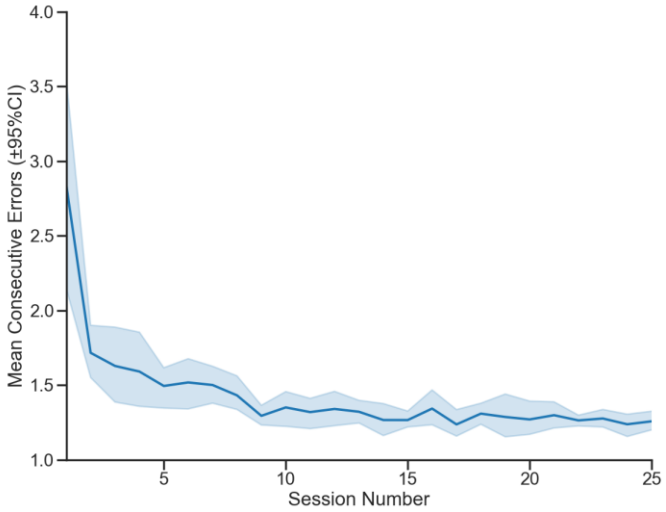

Figure 10. Mean number of perseverative errors on incorrect trials before completing the trial successfully in Experiment 4B. The dramatic drop within the first few sessions indicates that the correction procedure did eliminate perseverative errors quite quickly. Monkeys stopped defaulting to a side bias with a constant 50% reinforcement rate. 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.

7. 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 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 could learn 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 test are identical except for their location on the screen.

7.1. Procedure

In Experiment 5, we repeated the location probes from Experiment 3, but monkeys were now only rewarded for correct responses (Figure 8, Exp. 5). Monkeys were presented with sessions of 160 trials until they reached two consecutive sessions at or above 85% correct, or until they completed 25 sessions without accuracy improvement, but the latter was not the case for any of the monkeys.

Subjects could still perform well in this task without copying 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.

7.2. 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), and showed significant learning over the first 7 sessions (Figure 11, Greenhouse-Geisser $F(2.867,14.335)=12.725$, $p<.001$). 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 copying the demonstrator's behavior, as demonstrated by

the mirrored videos in Experiment 3, so it is not likely 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.

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.

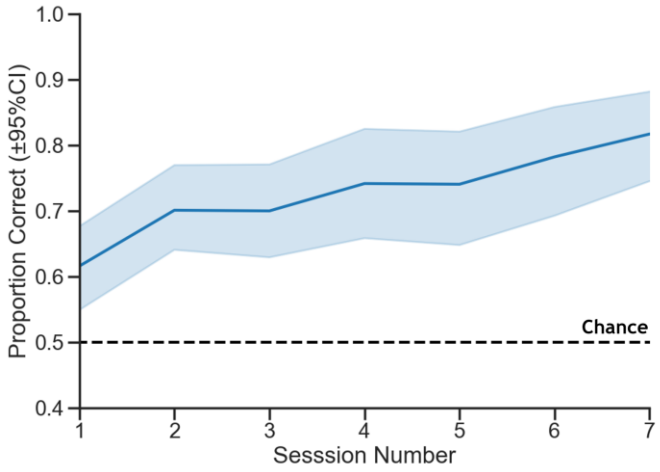

Figure 11. Performance results on location trials from Experiment 5 for the first 7 sessions, which was the minimum number of sessions to criterion. All subjects reached criterion on the task within 24 sessions. Solid line represents the mean proportion of trials completed correctly on the first attempt (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 chance level.

8. 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 at 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.

8.1. Procedure

As previously, the procedure from Experiment 2 was first replicated for each monkey until they completed two consecutive 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 2,048 trials was replaced with a probe trial in which the monkeys were presented 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 Figure 6, mirrored intact probe trials). Probe trials were always rewarded regardless of subject response. This resulted in 256 mirrored probe trials per monkey.

8.2. 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 (Figure 12, mirrored probes, one-sample t-test against choosing at random: $t(5)=-2.817$, $p=.019$). Meanwhile, subjects maintained accuracy on unmirrored training trials (Figure 12, training trials, one-sample t-test: $t(5)=13.755$, $p<.001$). This replication corroborates our previous interpretation that monkeys were not performing better than chance on the training trials by copying the demonstrator monkey, but rather by learning an arbitrary association between each video and a response location.

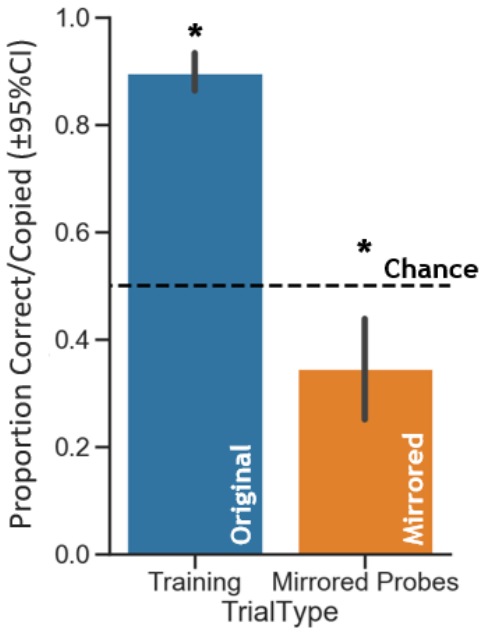

Figure 12. Accuracy on training trials and horizontally mirrored probe trials. Unmirrored training trials were differentially reinforced and comprised 7/8ths of trials. Mirrored probe trials were always reinforced regardless of subject response and comprised the remaining 1/8th of trials Significance indicators (* for significant) refer to a one-sample t-test with α=.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.

9. General discussion

Adult male rhesus monkeys did not learn to copy the choices of a demonstrator shown in video, even after extended training and various efforts to facilitate learning. While monkeys did learn to condition their left-right responses on the videos, our experiments with mirror image videos indicate that they were memorizing idiosyncratic features of the videos rather than copying the demonstrator's behavior.

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 (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, monkeys still failed to copy, learning the pairs by trial and error instead. 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 exposure to that pair. This distinction may suggest that social learning is more readily engaged in rhesus monkeys for habit learning rather than explicit learning of novel cognitive rules. In other words, monkeys may benefit more from observing many demonstrations of each

associative pairing without needing to follow an explicit rule of copying the demonstrator, although this account would contradict the cognitive imitation on a serial position learning task reported by Subiaul et al. (2004).

Rhesus monkeys readily solve a match-to-sample task where the correct response is shown among several distractors and indicated by a flashing border at training (Brady & Hampton, 2018). When the images were shown again after a delay and without a border, monkeys were able to identify the image that was previously presented with a border. This demonstration that a visual cue can guide monkeys' choice of image at test, makes it all the more surprising that monkeys did not copy the behavior of a demonstrator, which one would presume might be at least equally salient. The video demonstrations used in this study may not have provided a sufficiently salient signal of the correct response in each trial, or the videos themselves may have been distracting and therefore counter-effective in comparison to simply highlighting the correct response.

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 attempted to address 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 result in monkeys copying

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.

Although rhesus monkeys appear to gather social information from edited videos in some circumstances (Paxton et al., 2010), it is possible that the monkeys in our study did not experience the videos as social stimuli at all. Even when our monkeys learned to attend to *something* in each video, they did not copy 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.

The demonstrator monkey filmed in these videos was also one of the six monkeys tested in this study, but he did not see any of the images used in the experiments during recording as those were edited into the videos later. 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 & de Waal, 2009). And while evidence from the mirror self-recognition test with monkeys has been debated in the literature (e.g., Anderson & Gallup, 2015; Chang et al., 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 rely on copying the demonstrator because adult male rhesus monkeys are not likely to copy from other competing adult male rhesus monkeys. Particularly, direct gaze is a threat signal in most primates (Lorenz, 2002), so the use of an adult male demonstrator may have discouraged subjects in this experiment from closely watching the demonstrator's actions. 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.

Adult male rhesus monkeys did not spontaneously engage in copying from a conspecific video to solve a two-choice discrimination task. Under some conditions, they falsely appeared to copy a demonstrator, but closer examination indicated that their learned associations did not really follow the demonstrator's behavior. Even after significant training, and when trial-and-error learning was not possible, monkeys did not match their response to the identity of an image selected 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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