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Mirror Image Equivalence in the Perception of Stimuli by Brown Capuchin Monkeys

(*Cebus apella*)

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An abstract of
A thesis submitted to the Faculty of Emory College of Arts and Sciences
of Emory University in partial fulfillment
of the requirements of the degree of
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Abstract

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Mirror image equivalence, or the inability to discriminate between mirror images, has been expressed in some nonhuman primates. It is hypothesized that humans are more adept at discriminating mirror images due to lateralization and hemisphere specialization in the brain. As demonstrated by children confusing letters of the English alphabet with their mirror image, mirror image discrimination may not be an innate ability, rather a learned ability, in humans. In the current study, we tested brown capuchin monkeys (*Cebus apella*) on both left right and up down mirror images in an oddity paradigm under a probe and a learning condition. We found no evidence that they can spontaneously discriminate both left-right and up-down mirror images, but they may have the capacity to learn to discriminate both. Future studies should look at learning over a longer period of time, and introduce more complex stimuli.

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Mirror Image Equivalence in Capuchins

Mirror Image Discrimination in Humans

Mirror image discrimination, the ability to differentiate between an image and its mirror image, has been studied in both humans and animals through a variety of methods. Interest in this topic was originally sparked by research in mental rotation, which showed that human's delayed response for objects that are more rotated from their original orientation was an expression of hemisphere specialization (Kohler, Hoffmann & Mauck, 2005; Burmann, Denhardt & Mauck, 2005). Mirror image discrimination became a new area to study hemisphere specialization in both animals and humans.

There are two types of mirror images: vertical, or up-down (UD) mirror images and lateral, or left-right (LR) mirror images. Humans are capable of discriminating between mirror images, yet it is not fully understood how this is accomplished. Feature-based theory states that objects are recognized by features independent of orientation (Corballis, 1988). Descriptions of objects that utilize features independent of orientation are called frame independent descriptions, and these do not differentiate an image from its mirror image. This may not be disadvantageous, because there is often no need to discriminate an image from its mirror image in nature. A frame independent description may be sufficient for mere object recognition, however the use of written language may require an understanding of orientation, as is the case with the letters p, q, b and d. The mental process that provides cues of orientation is not fully understood, yet Corballis (1988) suggests that parity, defined as the understanding of left-right orientation, may be an essential component to mirror image discrimination. Parity is dependent on an inherent understanding of left versus right in relation to oneself. This directional sense of space may develop in humans due to handedness or asymmetrical scanning, and it may be acquired when learning to read.

Corballis and McMaster (1996) attempted to test the influence of parity on mirror image discrimination. Participants were shown rotated letters, and instructed to judge if the letters were normal or backwards, a measure of mirror image, and if a dot was placed to the left or right of the letter, a judgment of parity. There were two conditions: the viewer centered condition, where the judgment was made with respect to the current orientation of the letter, and the letter centered condition, where the judgment was made with respect to the correct orientation of the letter. When comparing these two conditions, they found that there was no difference in subjects' reaction times. Reaction times were slower for backwards letters, which suggests the backwards orientation had to be corrected before answering the question, likely by mental rotation.

Although Corballis and McMaster's (1996) study did not conclusively establish a relationship between parity and mirror image discrimination, it suggested a relationship between mental rotation and mirror image discrimination. Past studies support this finding in humans, such as Corballis and McLaren's (1984) study. They used the letters p, q b, and d at varying angular orientation and asked participants to discriminate between either LR or UD mirror images. Increased reaction time for both types of mirror images in comparison with control images suggested mental rotation was necessary for both UD and LR mirror images. Some animals, such as pigeons (*Columba livia*), demonstrate a time independent rotational invariance, such that their ability to discriminate images at differing orientations does not produce a time lag, as it does in humans (Burmann, Dehnhardt & Mauck, 2005; Koheler et al., 2005). Studies in rhesus macaques (*Macaca mulatta*) and lion tailed macaques (*Macaca silenus*) suggest that nonhuman primates do not demonstrate rotational invariance or mental rotation (Burmann, Dehnhardt & Mauck, 2005; Koheler et al., 2005). The authors hypothesized that nonhuman primates may possess a mechanism that is an intermediate between rotational invariance and mental rotation. This may be reflective of the evolution of mental rotation in humans, which may affect our ability to discriminate mirror images.

Mirror image discrimination is not an ability people are born with; rather, it appears as if it is a capability that children learn around the age of four or five. This has been studied in the context of learning to read and write, because children often confuse mirror image letters, such as b and d, at this stage (Casey, 1986). The ability to discriminate mirror images appears to differ on the individual level, yet generally children improve with age. Children can be classified as level one, incapable of spontaneously discriminating or learning to discriminate, level two, incapable of spontaneously discriminating but able to learn how, or level three, spontaneously discriminating without instruction. Studies investigating why level one children cannot learn to discriminate suggest that a lack in selective attention and systematic search techniques interfere with their ability to effectively scan for elements essential to mirror images (Casey, 1986). Analysis in the differences in abilities from level two to level three stresses the importance of attention again, and may also be influenced by the maturation of left-right discriminating abilities. Although the concept of left and right is present in one year olds, as shown by side preferences, it is not until two years old that children can discriminate, and it may take up to three or four years of age to solidify this concept (Casey, 1986).

Although some research suggests that young children are not good at discriminating mirror images, their poor performance may be attributable to a poor experimental design (Braine & Fisher, 1988). Typically, mirror images are presented side by side, which may make discriminating them harder for children than if they were presented one at a time, or stacked vertically. When children are tested on mirror images that are displayed separately, they are able to learn to discriminate them and later transfer this knowledge to a design where two stimuli are presented simultaneously. One hypothesis regarding the difficulty with the side by side design suggests that by displaying the mirror images side by side, children assess the orientation of the images as facing towards or away from each other, instead of as facing right or left. To test this, children were asked to perform a discrimination task with nonmirror images that were left or right oriented. They performed as poorly on this task as they did on the side by side mirror image task, supporting this hypothesis that they were judging the pictures using facing towards or facing away orientation (Braine & Fisher, 1988). Therefore, presenting two mirror images side by side may not facilitate their discrimination in a mirror image discrimination task, and this potential problem was taken into account in the design of the current study.

Mirror Image Discrimination in Nonhuman Primates

Mirror image discrimination has been tested in nonhuman primates in an attempt to trace the evolution of this ability in humans. A variety of nonhuman primate species have demonstrated mirror image equivalence, or the inability to discriminate between an object and its mirror image (Achin & Corballis, 1977). However, the results on mirror image discrimination tasks with different nonhuman primate species vary. Mirror image equivalence is demonstrated by the reaction of the inferotemporal (IT) cortex, a structure responsible for visual object recognition, to mirror images. The firing rate of the IT cortex changes as it processes new stimuli. Yet, in rhesus macaques, the firing rate did not differ significantly for LR mirror images, suggesting that the macaques had difficulty differentiating the images (Rollenhagen & Olson, 2000). A similar study was conducted in humans that yielded the same results (Baylis & Driver, 2001). In addition to recording IT cortex activity, this human study assessed subjects' perception of similarity between the presented mirror image pairs. Subjects were more likely to judge LR mirror images as more similar, which may explain the constant firing rate of the IT cortex.

Yet, in a study with baboons, (*Papio papio*), when the stimuli were restricted to one visual field, subjects were capable of discriminating the mirror images (Hopkins, Fagot & Vauclair, 1993). However, once the mirror images were shown bilaterally, the baboons' reaction times and accuracy declined. This study, along with the majority of studies on mirror image discrimination, made use of a match-to-sample paradigm in which a probe image is displayed on a screen followed by the simultaneous display of two images, one of which matches the probe image. The baboons' poor performance may be related to the match-to-sample design. It is possible that the baboons had difficulty with the simultaneous presentation of mirror images, just as human children do (Braine & Fisher, 1988). Therefore, in the current study, images are not presented just side by side and a paradigm other than match-to-sample was employed.

Neuroanatomical Hypotheses on Mirror Image Equivalence in Nonhuman Primates

Mirror image equivalence in nonhuman primates may be explained by differences between their brains and human brains. A case study on a person, referred to as GR, with right inferior parietal damage revealed this area of the brain's involvement in mirror image discrimination (Priftis et al., 2003). GR was able to recognize objects and their orientation, but could not discriminate between mirror images, suggesting that these functions are controlled by different areas in the brain. Differences between human and nonhuman primate brains in the right inferior parietal region may explain nonhuman primates' difficulty with discriminating mirror images.

Another key element of a human's brain that aids in mirror image discrimination is lateralization and hemisphere specialization. It is important to look at lateralization in animals, particularly nonhuman primates, in order to fully understand the evolution of lateralization in human brains (Hamilton, 1983). Empirical evidence suggests that, despite nonhuman primates' lack of language, they do exhibit hemisphere specialization (Hopkins, Washburn & Rumbaugh, 1990). For example, the right hemisphere specializes in facial/expression recognition and memory while the left hemisphere specializes in object recognition and discriminating lines oriented at different angles (Hopkins, Washburn & Rumbaugh, 1990; Hamilton & Vermeire, 1988; Hamilton, 1983). However, these correlations are analogous to those in humans, and would not suggest a difference in mirror image discrimination capabilities (Hamilton, 1983). Some nonhuman primates also exhibit handedness, as assessed by the TUBE test, where they are given a tube with a reward inside and the hand the primate uses to extract the reward is considered the dominant hand (Phillips & Hopkins, 2007). If handedness plays a role in the development of parity, the understanding of left versus right, as theorized by Corballis (1988), it is possible that nonhuman primates possess this. However, this should aid in mirror image discrimination, not lead to mirror image equivalence.

Studies on the neuroanatomy of the monkey brain in regards to mirror image equivalence were pioneered by John Noble (1968). In order to locate specific brain areas that may contribute to mirror image equivalence in nonhuman primates, Noble conducted a series of experiments on rhesus macaques with particular brain lesions. He monocularly presented the macaques with mirror image stimuli, rewarding the monkey for choosing one stimulus labeled the positive image. The other stimulus was labeled negative, and was not rewarded. Then the macaques were tested on the same images with the opposite, untrained eye. Both the positive and negative images were rewarded, so there was no opportunity for learning. His subjects either had no surgery or one of the following surgeries: sectioning of the optic chiasm, sectioning of both the corpus callosum and the optic chiasm, sectioning of one optic tract, or sectioning of both the corpus callosum and the anterior commissures.

The optic chiasm sectioned macaques yielded the most interesting results. He noticed that they were neglecting the image on the same side as the open eye, and when this was the correct response, they would make gross head movements to locate the stimulus. From this, Noble concluded that there was a blind spot on the same side of the visual field as the respective eye. Therefore, there was a biasing of attention so that the image was projected to the ipsilateral side of the brain only. This pattern of blindness was later confirmed in other studies (Lehman & Spencer, 1973). The discrimination of LR mirror images is based on an internalized concept of left and right, yet the chiasm sectioned macaque only received direct input from part of a visual field and this may have affected its representation of left and right. The results seem to support this claim, because the interocular transfer showed a paradoxical preference for the negative stimulus, and these results have since been replicated (Lehman & Spencer, 1973). Noble hypothesized that this may be mediated by the anterior commissure and the corpus callosum.

The optic chiasm and corpus callosum sectioned macaque also showed a paradoxical preference for the negative stimulus. Because this macaque had its corpus callosum severed, this suggests that this structure is not responsible for the paradoxical interocular transfer. Therefore, Noble revised his hypothesis to cite just the anterior commissure as the cause of the reversal in preference. This was supported by the results from the corpus callosum and anterior commissure sectioned macaques, who demonstrated veridical interocular transfer, meaning that they preferred the positive stimulus. Veridical transfer likely occurs because the macaques receive direct input in both hemispheres, but there is no secondary information input from a transfer of information across hemispheres. Other studies support this claim by showing that monkeys with their anterior commissures severed performed better in terms of both accuracy and speed on LR mirror image discrimination tasks than monkeys with sectioned optic chiasms or corpus callosums (Achin & Corballis, 1977). Finally, the normal monkeys and optic tract sectioned monkeys also exhibited veridical transfer, because only one hemisphere received direct visual input, and the other hemisphere only received information secondarily from interhemispheric crossing (Noble, 1968).

The results of this study on interocular transfer can be extrapolated to explain the problems of mirror image equivalence in experiments with binocular designs. As demonstrated by the optic chiasm sectioned monkey, the presence of homotopic commissures, specifically the anterior commissure, causes a secondary input that reverses the information from the direct visual input. The positive representation of the image is received from interhemispheric transfer and the negative representation is received from direct visual input. Therefore, an image becomes impossible to discriminate from its mirror image, and when one is rewarded over the other in an experimental setting, the subject associates the reward with both orientations of the image. Therefore, in order to discriminate binocularly presented LR mirror images, the primary visual input must override the transfer of information across homotopic commissures to the opposing hemisphere (Noble, 1968).

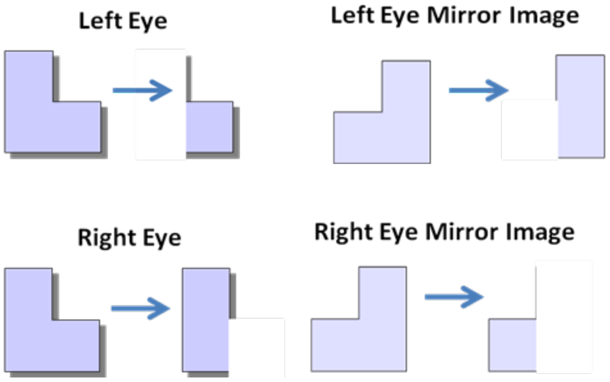
However, Noble’s explanation of his results has been questioned (Hamilton & Tieman, 1973; Hamilton, Tieman & Brody, 1973). One main flaw in his argument is that he assumes that nonhuman primates’ mirror image discrimination abilities are consistent and well documented, when the reality is that they sometimes exhibit mirror image equivalence and sometimes are capable of discriminating them (Hamilton, Tieman & Brody, 1973). Another problem with Noble’s hypothesis is that a cell typically responds to a stimulus of the same orientation, whether the input is direct or cross hemisphere. This is shown with smaller mirror images, which are transferred veridically in optic chiasm sectioned monkeys (Hamilton, Tieman & Brody, 1973). It is possible that the homotopic fibers that Noble sites as the cause for the image reversal may not be as interconnected with the visual field as originally believed.

To account for these shortcomings in Noble’s neuroanatomical hypothesis, two behavioral mechanisms have been proposed: the coding hypothesis and the masking hypothesis (Hamilton & Tieman, 1973; Hamilton, Tieman & Brody, 1973). The difference between the behavioral mechanisms and Noble's anatomical mechanism is that the anatomical model must operate continuously, whereas the behavioral model is more flexible. The first behavioral mechanism, the coding hypothesis, suggests that the blind spots caused by the severing of the optic chiasm may provide extra cues that aid in mirror image discrimination tasks (Hamilton & Tieman, 1973; Hamilton, Tieman & Brody, 1973). This would affect performance on LR mirror image discrimination, but not UD because the blind spots exist in a centralized location on one side of the visual field. Thus, flipping an image vertically would leave the blind spot in the same place and would not provide extra cues for discrimination purposes. To test this theory, polarizing light filters were used to minimize the effects of the blind spots. If the monkeys were reliant on these blind spots for LR discrimination, their accuracy should decrease with the filters, and the UD should be unaffected. However, their performance on both the UD and the LR did not differ significantly with the filters compared to without the filters, suggesting that the monkeys do not use the blind spots as predicted by the coding hypothesis (Hamilton & Tieman, 1973).

The blind spots may still affect mirror image discrimination by masking opposite halves of the pattern for either eye, which is the basis of the masking hypothesis (Hamilton & Tieman, 1973; Hamilton, Tieman & Brody, 1973). The ipsilateral side of the stimulus is covered by the blind spot, so if the left eye is looking at the stimulus, the left side of the stimulus is blocked. This causes an asymmetrical focus of attention as attention shifts to the contralateral side of the stimulus because it is more visible. When the mirror image of the stimulus is shown, the side that was previously visible is now masked by the blind spot. Therefore, masking essentially transforms the images into nonmirror patterns, thus making the task a simple pattern discrimination task (see Figure 1). To test this theory, normal monkeys were tested on mirror images where the ipsilateral side of the stimulus was physically covered, as it would be if they had blind spots caused by optic chiasm sectioning. The monkeys performed significantly better with the physical masking, thus supporting the masking hypothesis.

Figure 1

The images portray the stimulus as is and the stimulus as seen when partially masked for the left and right eye respectively.



The masking hypothesis emphasizes the importance of attention on mirror image discrimination, and this effect has been replicated in studies with humans. In one such study, subjects were presented with two stimuli simultaneously, one was enclosed in a cuing square and one was not, and they were told to pay particular attention to the stimulus in the cuing square (Stankiewicz, Hummel & Cooper, 1998). They were then shown a probe image that was either the image from the cuing square presented in either its original form or mirror image, the ignored image also presented in original and mirror image form, or an image they had not previously seen. They found that the ignored images were only remembered when they were presented in their original form, suggesting that object recognition is sensitive to LR reflection when the subject is not paying particular attention to the original image. This study highlights the importance of attention in mirror image discrimination tasks.

Difficulty Discriminating Left-Right Mirror Images in Nonhuman Primates

Although many species of monkeys have difficulty with both UD and LR mirror images, some may be more adept at distinguishing between UD mirror images (Hamilton, Tieman & Brody, 1973; Rollenhagen & Olson, 2000). This was demonstrated in a study where rhesus macaques had to discriminate between LR mirror images in a match-to-sample design with the addition of an uncertainty option (Hamilton, Tieman & Brody, 1973). This option removed the incorrect stimulus from the display of the two possible response stimuli, thus revealing the correct response. The rhesus macaques chose the uncertainty response 43% of the time, suggesting that they had difficulty discriminating the LR mirror images (Washburn, Smith & Shields, 1999). This difficulty is opposite of that in humans; mental rotation for LR mirror images was quicker because they are more similar to the original image, and therefore require less time to mentally rotate (Corballis & McLaren, 1984). Perhaps the similarity between LR mirror images that facilitates discrimination in humans actually hinders it in nonhuman primates.

This discrepancy in performance on LR mirror images compared to UD mirror images has been further explored at the neuroanatomical level (Noble, 1968; Baylis & Driver, 2001; Rollenhagen & Olson, 2000; Achin & Corballis, 1977). Noble (1968) was the first to note that bilateral symmetry in the nervous system, interhemispheric commissures, and the corpus callosum reverse the topographic image of the stimulus in the brain. These brain structures that he names are homotopic connectors because they join symmetrically placed areas of the cortex. If the same stimulus is presented to both eyes individually, it will be perceived differently by each eye such that the two images in the brain form mirror images. Noble hypothesizes that this is caused by transfer of information across the homotopic commissures. Comparatively, if LR mirror images are presented to each eye, then the resulting representations in both hemispheres would be identical images. Essentially, transfer of information across the homotopic commissures creates reflected images. However, UD mirror images do not experience this paradoxical reversal. Unlike the left and right visual fields, the upper and lower visual fields send their information to areas in one hemisphere that are connected to respective upper and lower areas in the other hemisphere. In this case, homotopic commissures do not cause a reversal in the image. This may explain why some nonhuman primates perform better on UD mirror image tasks than LR.

The Current Study and Our Hypothesis

The current study analyzes mirror image equivalence in brown capuchin monkeys (*Cebus apella*). Prior to this study, capuchins have not been the subject of any mirror image discrimination research. However, they are a good candidate for this research because they have asymmetries in their brain, suggesting the existence of lateralization, which is hypothesized to be the key element of human brains that aids us in mirror image discrimination. Capuchins have asymmetrical cerebellums, a part of the brain that is responsible for coordination of motor skills to cortical motor areas and the processing of information to the prefrontal cortex. This asymmetry correlates with handedness, and may be associated with the evolution of population-level handedness, a prime example of lateralization (Phillips & Hopkins, 2007). Capuchins also have population-level left-frontal petalia, such that their left frontal cortex is larger than their right (Phillips & Sherwood, 2007). This asymmetry suggests greater hemispheric division of function, which may aid in mirror image discrimination as explored in the current study. Capuchins also have asymmetry in the sylvian fissure, a collection of nerve fibers that divides the parietal and frontal lobes from temporal tissue, that is analogous to human asymmetries in this area (Liu & Phillips, 2009). If this structure plays a role in mirror image discrimination, the similarity in its asymmetry in humans and capuchins could suggest that capuchins may be capable of mirror image discrimination like humans.

The purpose of the current study is to assess mirror image discrimination abilities in this species. We tested six brown capuchin monkeys (*Cebus apella*) on both UD and LR mirror images in an oddity task paradigm, where the images were presented in both probe trials and learning trials. Due to capuchins' unique brain asymmetries and hemisphere specialization, we hypothesized that they would be capable of spontaneously discriminating mirror images in the probe trials. If they were unable to do so, we predicted that they would be capable of acquiring this ability in the learning condition. More specifically, we hypothesized that they would perform better on the UD than the LR mirror image discriminations task, as demonstrated in the literature. Finally, we predicted that the oddity paradigm would be an accurate indicator of whether the capuchins possess this ability, due to their success in previous studies using this paradigm (Pokorny & de Waal, 2009).

Past research indicates a few methodological problems that we attempt to address in the current study. The role of attention on mirror image discrimination has been emphasized in research on humans, so to ensure subjects are paying attention, oddity task control trials of non mirror images will be used to assess attention level (Stankiewicz, Hummel & Cooper, 1998). Although originally assumed to be problematic, the size and angularity of the stimuli do not affect mirror image discrimination, therefore our letter stimuli should be appropriate (Lehman, 1973). Additionally, research suggests that simpler stimuli may enhance discrimination, and the black, block letters used in the current study are indeed simple (Lehman, 1973). Finally, decreased performance on LR images versus UD images may be due to a biasing of attention. Apparatuses may draw attention to the lower corners of the stimuli, thus making UD discrimination easier than LR (Hamilton & Tieman, 1973). By randomizing both the location of individual stimuli and the general formation of all the stimuli, this should control for biasing of attention by the computer screens.

Methods

Subjects and Housing

Subjects were three adult and three subadult brown capuchin monkeys (*Cebus apella)*, from two separately housed social groups at Yerkes National Primate Research Center. Training began in November of 2009, and testing ended in March of 2010. Subjects were two females from group 1, named “Winnie”, age 26, and “Wilma”, age 13, one male from group 1, named “Wookie”, age 5, one female from group 2, named “Bailey”, age 10, and two males from group 2, named “Benny”, age 6, and “Gonzo”, age 4. Group 1 and group 2 were housed in the same facility, separated by an opaque barrier such that the two groups had no visual contact. The monkeys had free access to the indoors and outdoors, and constant access to monkey chow and water with supplemental trays of fruit and bread in the evenings. Testing occurred between 10:00 and 18:00 hours, with each pair only tested on this task once a day, and up to three times a week. All subjects were also used in other studies occurring simultaneously, such that most subjects were tested on different experiments daily. Testing pairs were created within groups such that closely affiliated monkeys tested together to ensure individual comfort.

Apparatus

A test chamber, measuring 155 x 64 x 58 cm, was rolled up to the capuchins' enclosure to allow the testing subjects to be separated from the rest of their group. The test chamber was divided in half by an opaque barrier with a small hole in the back to block view of the other monkey's test screen, but still allowed visual contact between the testing pair for comfort. Touch screen sensitive PC computers, mounted on a rolling cart, were presented in front of the testing chamber, and the front of the test chamber had arm holes cut out to allow the monkeys to reach out of the chamber and touch the screens. The computer carts also contained automatic pellet dispensers to dispense a reward of either Kix® cereal or Purina® LabDiet Primate Pellets as a reward. Visual Basic 6.0 was used to program the test, control reward distribution, control an appropriate sound playback, and collect data.

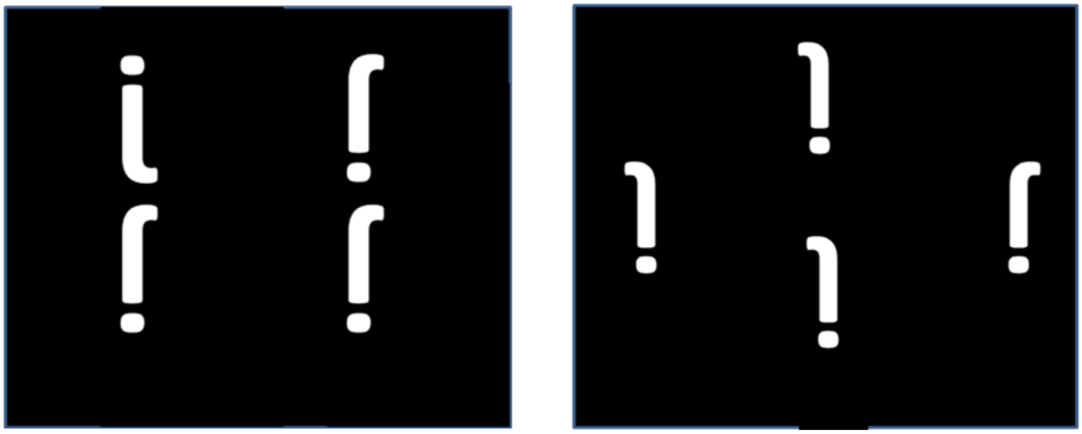
Stimuli

Stimuli used for training were two dimensional lower case letters of the English alphabet. The letters were fit into a 8.4 square cm, 300 x 300 pixel black square, with the letters displayed in white font. All letters were created using Adobe Photoshop 6.0. The stimuli used in testing trials were the same size and font, but all letters were upper case. Lower case letters were used in training to avoid over familiarizing the subjects with the stimuli. All letters were presented in their original form, LR mirror image, UD mirror image, and inverted both ways in order to increase the number of possible test trials. Therefore, the three comparison images could be letters that were reflected LR, UD, or both, and the odd stimulus was either the LR or UD mirror image of that image (see Figure 2). This was possible because the subjects were unfamiliar with the "correct" orientation of the letters.

Figure 2

Left: an example of an UD trial using an UD and LR reflected j as the "same" stimulus.

Right: an example of a LR trial using an UD reflected j as the "same" stimulus.



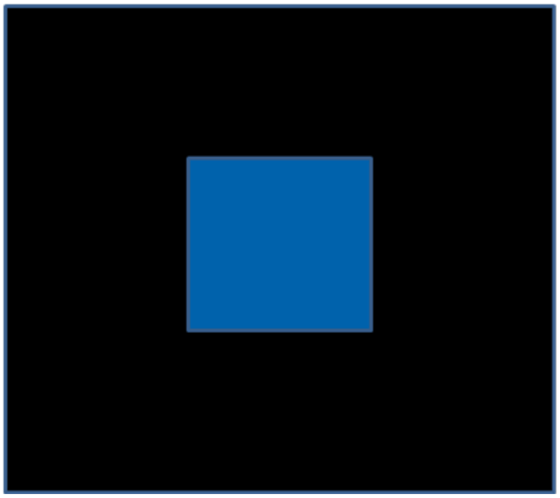
Procedure

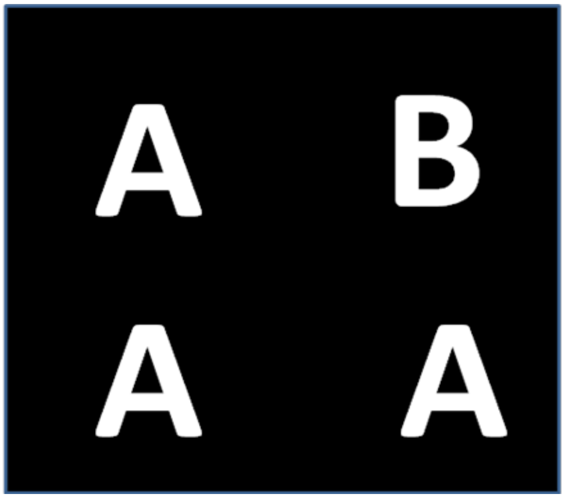
The experiment was conducted using an oddity paradigm created by Jen Pokorny (Pokorny & de Waal, 2009), a procedure with which all six monkeys had been previously trained. The stimuli for this training phase were colored, two dimensional clip art images. The beginning of a trial was marked by a square in the center of the screen that had to be touched in order to start the trial. Then four images would appear on the screen, either in a square or diamond layout. Three of these images were identical and one was different, or “odd”, with the odd stimulus being the correct choice. The location of the odd stimulus and the type of layout, square or diamond, was randomized for each trial. If the correct response was chosen, a high pitch tone would sound, a reward would be delivered, and the monkey would move on to the next trial. If the incorrect response was chosen, a low pitch noise would sound, no reward would be delivered, four seconds would be added to the intertrial interval, and the monkey would repeat the same trial until he/she answered correctly or failed to answer correctly four times in a row. After four unsuccessful attempts, the monkey would move on to the next trial and receive no reward. Only first attempt responses were included in data analysis. Trials were aborted if the monkey either refused to touch the initial square, or touched the initial square but failed to touch one of the four images in the allotted time of 30 seconds after trial initiation. An aborted trial would be followed by a low pitch tone and no reward, and it was not repeated. Aborted trials were not included in the data analysis.

During testing, the experimenter stood behind the touch screens so as not to influence subjects’ choices. The experimenter would monitor behavior and attention, to ensure the subjects were safe and actively engaged in the experiment. If a subject appeared distracted or uncomfortable, the experimenter would stop the session.

Figure 3

An example of what a control trial would look like. It begins with the picture on the left, and after the subject touches the blue square, it proceeds to the picture on the right.





Clip Art Oddity Training

All six subjects were trained on the oddity task using clip art prior to the start of the current study. A set of 560 images total was used throughout the stages of training, starting with just 20 images as the identical images and one of the remaining 540 images as the odd image. As the subjects progressed, the set of identical images grew to 50, and eventually the odd and identical image possibilities were switched such that the odd image came from the one of the 50 previously identical images. After this crucial switch, the odd image could be any of the 560 while the identical image came from a set of 100, and over time groups of 100 stimuli were added to this repertoire. In the next step, the odd image and the identical images were selected randomly from any of the 560 images. Finally, additional clip art images were added to bring the total to 680 images. Subjects had to perform this task with at least 60% accuracy for two consecutive sessions before moving on to the next stage.

This previous training was significant to the current study for two reasons. First, it was a means to train each individual on the oddity task. Second, the clip art images were used as controls in the letter discrimination training phase of the current study.

Letter Discrimination Training

Before subjects could perform a mirror image task, they were trained on discriminating the stimuli, all possible inversions of lower case letters from the English alphabet. The oddity task was used such that three images of the same letter were displayed with one image of a different letter. Letters that were UD or LR mirror images of each other, such as p’s and q’s, or n’s and u’s, were excluded from the letter discrimination trials. UD mirror images were included in this training session, along with clip art trials, as described above, as a control to monitor attention. Each session consisted of twenty-five trials of letter discrimination, twenty-five trials of UD mirror image discrimination, and twenty-five trials of clip art. Subjects had to reach 60% accuracy for two consecutive sessions on the letter discrimination. Before subjects moved on to the testing trials, they were given anywhere from two to four sessions of training on upper case letters, depending on individual differences. The format was exactly the same, but the stimuli were upper case letters, as they would be in the testing trials. These extra sessions were included to ensure transfer from the lower case to upper case letters. Once again, the criterion subjects met before moving on was at least 60% accuracy on the letter discrimination for two consecutive sessions.

Mirror Image Discrimination Task

There were two stages of experimental sessions. In the first stage, both LR and UD mirror images were presented as probe trials such that subjects were rewarded on their initial response, despite accuracy, and the trials were not repeated. There were twenty trials of each mirror image type. The control was the letter discrimination, as presented in the training, and there were forty trials of this. In order to include a subject's data, his/her performance on the control must have been at least 60% accuracy, which ensured the subject was paying attention. Because there was no opportunity to learn in this design, each subject spent three sessions on the probe trials. "Wilma" was the exception, performing five sessions, because she did not pass criteria on one session, and did not perform the full 60 trials in two of the sessions. With the total of five sessions, "Wilma" then passed criteria for paying attention and had enough trials of mirror images to compare her performance with the rest of the group's performance.

The next step was to present the UD and LR mirror images such that only the correct response was rewarded, and incorrect trials were repeated up to four times or until a correct response was given. Fifty mirror image trials, twenty-five of each type, and twenty-five control trials were presented. This design gives the subjects an opportunity to learn to discriminate, so that if they were unable to discriminate spontaneously in the probe trials, they may show a learning curve and begin to discriminate in this learning condition. The number of sessions each subject performed varied, depending on how quickly they progressed through the training sessions. “Winnie” performed five sessions, “Wookie” performed three sessions, and “Gonzo” performed six sessions.

Data Collection and Analysis

All data was recorded via Visual Basic 6.0. Each trial recorded information on the individual being tested, the experimenter running the test, the date, the trial condition (training, training with upper case letters, testing with probe condition, testing with learning condition), session number, the identity and location of the odd stimulus, latency in response (in msec), the image and location selected by the subject, and whether the trial was correct, incorrect or aborted. The dependent variable was accuracy, incorrect versus correct on first trial attempts, and the independent variable was the type of trial presented, UD mirror image, LR mirror image, or letter discrimination.

We ran a Heterogeneity G-test to see if performance differed significantly from chance both within individuals and across individuals for both the probe and the learning conditions. This statistic compares performance with random chance, in this case 25% because there were four options, similar to a chi-square test, but the G-test takes into account individual contributions. The data were also analyzed within subjects using a paired samples t-test to see if there was a trend for better performance on one type of mirror image discrimination for both the probe and the learning conditions. All sixty trials of the probe condition were analyzed, and sixty trials of the learning condition were analyzed in order to accurately compare across conditions.

Results

We analyzed the results for the probe and learning conditions separately, and then compared performance on these two conditions within individuals. There were sixty trials of both UD and LR mirror images for each of the six individuals in the probe condition. A binomial test showed that a score of 37% correct or better on a set of sixty trials would be significantly above chance performance. We used an alpha level of .05 for all statistics.

We ran a Heterogeneity G-test to see if the subjects performed above chance overall on either LR or UD mirror images. For the sixty trials of LR mirror images (*M* = 14.67, *SD* = 4.68), we found that none of the individuals were significantly above 25% chance, and “Wilma” was significantly below chance (see Table 1a). Despite this deviation, the heterogeneity test was nonsignifcant, thus the data were homogenous, and we were allowed to use the G pooled value ($G_h(5) = 10.48$, *p* = .0628). Performance across individuals was also nonsignificant ($G_p = .0596$, *p* = .8072), indicating that the group did not perform above chance. For the 60 trials of UD mirror images (*M* = 18.17, *SD* = 1.72), no individuals were significantly above chance (see Table 1b**)**. The heterogeneity test was nonsignificant, suggesting the data were homogenous ($G_h(5) =$ 1.16, *p* = .9483). Across individuals, performance for UD was significantly above chance ($G_p = 5.13$, *p* = .0236). We wanted to see if performance within individuals was better for UD mirror images than for LR mirror images. An one tailed, paired samples t-test showed that there was a significant difference (*t*(5) = -2.24, *p* = 0.038). The difference was in the expected direction, such that performance on UD (*M* = 18.17, *SD* = 1.72) was greater than performance on LR (*M* = 14.67, *SD* = 4.68).

We repeated the same tests with the learning condition, in which subjects were only rewarded for correct answers. Only three out of the six subjects, the best performers, performed sessions in the learning condition, due to time constraints. For LR (*M* = 22.00, *SD* = 2.00), two of the three subjects performed significantly above chance (see Table 1c). Across individuals, performance was significantly above chance ($G_p = 12.01$, $p < .001$). The heterogeneity value was nonsignificant, therefore the data was homogenous ($G_h = .57$, $p = .7502$). On UD (*M* = 24.00, *SD* = 2.00), all individuals performed significantly above chance (see Table 1d), and thus as a group performance was also significantly above chance ($G_h = .56$, $p = .7573$, $G_p = 19.48$, $p < .001$). Once again, we compared performance within individuals to see if performance on UD mirror images was better than LR mirror images, but this difference was nonsignificant ($t(2) = -1.732$, $p = .1125$).

To compare performance on the probe condition with performance on the learning condition, we conducted a sign test. We found that neither performance on probe UD compared to performance on learning UD ($p = .125$) nor performance on probe LR compared to performance on learning LR ($p = .125$) were significantly different (see Figure 4).

Table 1. G Values for LR and UD in the Probe and Learning Conditions

Table 1a

Results for LR mirror images in probe condition

Probe Left Right Trials			
Subject	% correct	G value	*p* value
Bailey	23.3%	0.0903	0.7634
Benny	26.7%	0.0876	0.7672
Gonzo	28.3%	0.3458	0.5565

Winnie	21.7%	0.3670	0.5447
Wookie	35.0%	2.970	0.0848
Wilma	11.7%	6.675	0.0098*

Note: *$p < .05$

Table 1b
Results for UD mirror images in probe condition

Probe Left Right Trials			
Subject	% correct	G value	*p* value
Bailey	30.0%	0.7682	0.3808
Benny	31.7%	1.349	0.2454
Gonzo	35.0%	2.970	0.0848
Winnie	28.3%	0.3458	0.5565
Wookie	30.0%	0.7682	0.3808
Wilma	26.7%	0.0876	0.7672

Table 1c
Results for LR mirror images in learning condition

Learning Left Right Trials			
Subject	% correct	G value	*p* value
Gonzo	33.3%	2.085	0.1488
Wookie	36.7%	4.002	0.0455*

Winnie	40.0%	6.494	0.0108*

Note: **p* < .05

Table 1d
Results for UD mirror images in learning condition

Learning Up Down Trials			
Subject	% correct	G value	*p* value
Gonzo	40.0%	6.494	0.0108*
Wookie	36.7%	4.002	0.0455*
Winnie	43.3%	9.542	0.0020*

Note: **p* < .05

Discussion

The results suggest that the brown capuchins were not capable of discriminating LR mirror images spontaneously, because under the probe condition, performance was not significantly above chance either within or across individuals. However, across individuals, performance was significantly above chance on UD mirror images. This was our original hypothesis, because the literature suggests that some species of nonhuman primates are more adept at discriminating UD mirror images than LR mirror images. However, at the individual level, no subjects performed above chance. It is possible that these results have been affected by the training trials. Before starting the mirror image discrimination task, each subject was trained on discriminating letters. UD mirror images were included in these training sessions, because we had expected the capuchins to perform well on them, and intended on using UD mirror images as a control. After weeks of training, we noticed that the capuchins were struggling with the UD mirror image trials, and decided that their performance was not good enough to use these trials as controls. Therefore, when the subjects reached the mirror image discrimination task as probe trials, they had previously seen UD mirror images, but not LR mirror images. It is possible that the group was significantly above chance on UD mirror image performance because of this previous exposure. Therefore, we concluded that the capuchins were not capable of spontaneously discriminating either LR mirror images or UD mirror images.

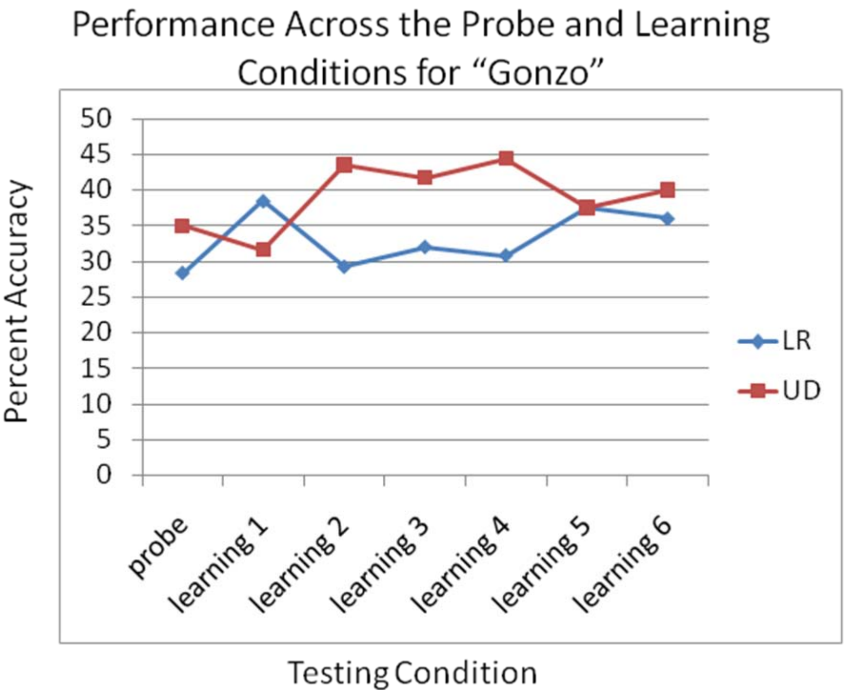
Performance within individuals in the probe condition did differ significantly for LR mirror images versus UD mirror images such that performance was higher on UD mirror images. This supports our hypothesis, however, it is possible that this was also affected by the previous exposure to UD mirror images. Subjects may have begun to learn to discriminate UD mirror images from the training trials, thus causing their increased performance on this mirror image type in the probe trials. However, this does not mean that the capuchins were better at discriminating UD mirror images than LR mirror images. As shown by the paired samples t-test in the learning condition, performance within individuals was not significantly different for UD mirror images compared to LR mirror images, and it was not even close to significance (p = .1125). One individual, “Wookie”, scored a twenty two out of sixty on both mirror image types, suggesting that he did not have an advantage at UD mirror image discrimination. This data suggests that, once subjects had more exposure to LR mirror images, their performance on this was comparable to their performance on UD mirror images. Thus, we concluded that the capuchins are not naturally better at discriminating UD mirror image than LR mirror images.

During the learning condition, we found that performance on both UD mirror images and LR mirror images was significantly above chance across individuals. With the exception of one individual, “Gonzo”, on the LR trials, individuals also performed significantly above chance on both types of mirror images. This was an improvement on both individual and group performance from the probe trials, which suggests that the subjects began to learn how to discriminate both types of mirror images.

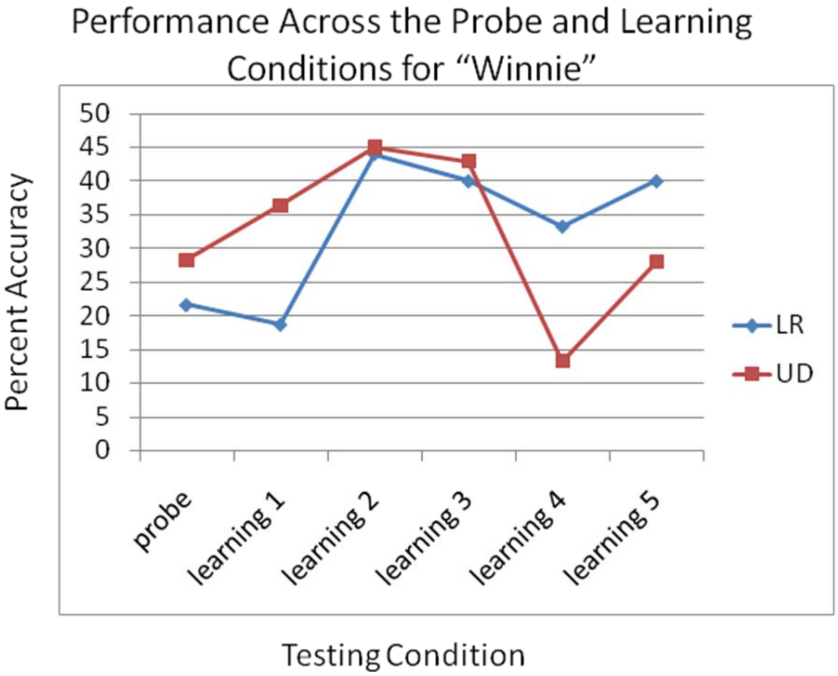
To see if learning was occurring, we compared performance across individuals on probe trials versus learning trials. Surprisingly, we found that the difference was not significant. However, this does not necessarily mean that the subjects were not learning. In the learning condition, performance on both UD mirror images and LR mirror images across individuals was significantly above chance. In the probe condition, neither was above chance. Also, due to time constraints, subjects who participated in the learning condition only partook in a couple of sessions, ranging from three to six. This short period of time may not be long enough to reflect a learning curve. Yet, it seems that it was long enough to affect some small change on both the individual’s and the group’s performance, since they performed significantly above chance (see Figure 4).

Figure 4: Graphs displaying three individual’s performance on the probe condition compared to each session of the learning condition.

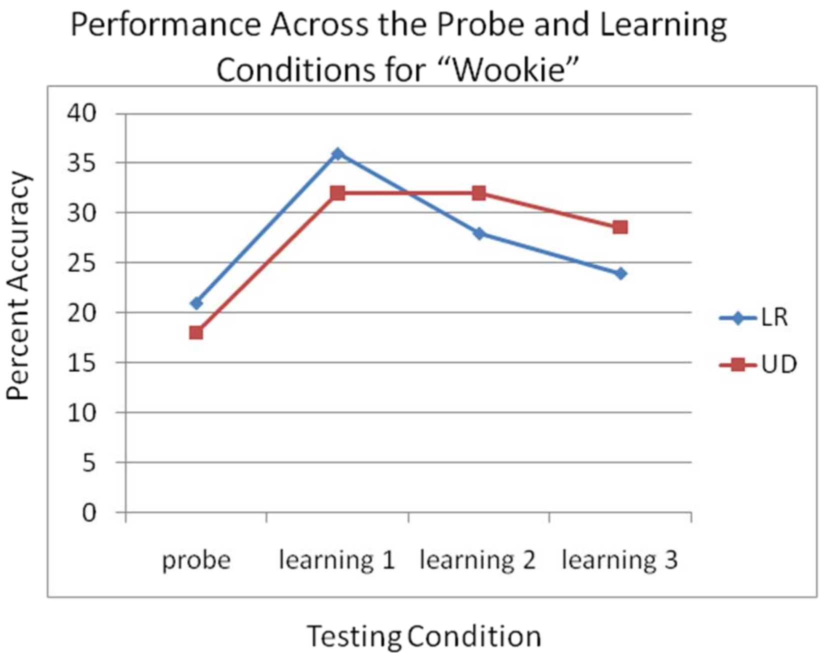
a. Percent accuracy on both LR and UD mirror images across the probe and learning conditions for “Gonzo”



b. Percent accuracy on both LR and UD mirror images across the probe and learning conditions for "Winnie"



c. Percent accuracy on both LR and UD mirror images across the probe and learning conditions for “Wookie”



Therefore, we concluded that the capuchins were not capable of spontaneously discriminating between either LR mirror images or UD mirror images, but may be capable of learning to do so. Although this is not what we had hypothesized, these results are not entirely surprising. Even in humans, a species that is very adept at mirror image discrimination, this ability is supposed to be learned, not innate (Casey, 1986). Children have trouble learning to write because they confuse letters with their mirror images. Perhaps people learn mirror image discrimination because it is necessary for their daily lives, as demonstrated by the English alphabet. Capuchins, on the other hand, have no ecological need to learn to discriminate mirror images. Their differences from humans in spatial abilities may be due to the fact that they have adapted to a three dimensional world (Burmann, Dhenhardt & Mauck, 2005). Mirror images have significance in two dimensions only. Therefore, nonhuman primates may not be so different from humans in their ability to learn to discriminate mirror images, they just have not had the need to do so in the wild. Thus, the implications of this study are that capuchins may possess the ability to learn to discriminate mirror images, much in the same way humans do.

Suggestions for Future Research

Future studies should extend the learning condition, in order to provide adequate time for subjects to learn. We plan to do so, and expect to see that the capuchins will eventually learn to discriminate both LR and UD mirror images. Also, ideally each subject should perform the same number of sessions in order to make comparisons across subjects, as well as within subjects. In the current study, only half of the participants progressed to the learning phase, so it would have be interesting to see how the remaining three subjects would have performed on the learning condition. These are all considerations that will be taken into account in the continuation of this study.

This study could also be repeated and improved by using a different set of stimuli, in order to see if more complex stimuli facilitate mirror image discrimination. We chose to use simpler stimuli because the literature suggested that increased complexity also increased the difficulty of discriminating mirror images (Lehman, 1973). However, having extra cues about change in orientation may in fact aid in mirror image discrimination. A follow up study could add the dimension of color to the stimuli, such that the letters would have a stripped pattern of alternating colors. When this image is reflected, the colors and pattern would also be reflected. There would then be three elements of the stimulus that would change upon reflection: the orientation of the letter, the placement of the color, and the direction of the stripped pattern. The addition of two extra elements that change upon reflection may aid in mirror image discrimination.

Another possibility is that the capuchins had a hard time discriminating the letters themselves. It took them several weeks, and in some instances, several months, to learn to discriminate between the letters. These capuchins are more familiar with clip art images, due to years of testing and training with those images. Therefore, a mirror image discrimination task with clip art images may be easier for them. Like the example with colored, patterned letters, the clip art stimuli would add the dimensions of color and pattern, potentially easing the discrimination task.

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