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Monkeys show recognition without priming in a classification task

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Abstract

Humans show visual perceptual priming by identifying degraded images faster and more accurately if they have seen the original images, while simultaneously failing to recognize the same images. Such priming is commonly thought, with little evidence, to be widely distributed phylogenetically. Following Brodbeck (1997), we trained rhesus monkeys (*Macaca mulatta*) to categorize photographs according to content (e.g., birds, fish, flowers, people). In probe trials, we tested whether monkeys were faster or more accurate at categorizing degraded versions of previously seen images (primed) than degraded versions of novel images (unprimed). Monkeys categorized reliably, but showed no benefit from having previously seen the images. This finding was robust across manipulations of image quality (color, grayscale, line drawings), type of image degradation (occlusion, blurring), levels of processing, and number of repetitions of the prime. By contrast, in probe matching-to-sample trials, monkeys recognized the primes, demonstrating that they remembered the primes and could discriminate them from other images in the same category under the conditions used to test for priming. Two experiments that replicated Brodbeck's (1997) procedures also produced no evidence of priming. This inability to find priming in monkeys under perceptual conditions sufficient for recognition presents a puzzle.

Keywords

implicit memory; nondeclarative memory; amnesia; repetition priming; categorization

1. Introduction

Seeing something makes it easier to see again. For example, if you saw a billboard partially obscured by a tree branch, you would likely identify the advertisement more readily if it were familiar than if it were novel. In the lab, this phenomenon is explored in studies of perceptual priming (sometimes called repetition priming; hereafter, priming; Tulving & Schacter, 1990). Subjects may be shown a set of novel images, the primes, and after a delay or manipulation, asked to name a number of degraded images, some that were seen previously, and others that are completely novel. Subjects typically show a memory effect in which they are more accurate or faster at naming the primed images than the unprimed images. Priming has been observed both with words, in which letters are missing (Tulving,

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Schacter, & Stark, 1982), and images, in which sections are missing or occluded (Mitchell, 2006; Snodgrass & Feenan, 1990).

A critical feature of theories of the organization of human memory is that priming is implicit. Subjects are better at identifying primed material even when they cannot explicitly remember that same material (Tulving & Schacter, 1990). Priming effects have been found to last from days (Tulving et al., 1982), to weeks (Mitchell & Brown, 1988), to years (Mitchell, 2006), long after subjects have forgotten the original prime. Unlike our ability to recognize images, which improves over childhood, priming is relatively constant over development (Parkin & Streete, 1988). Priming is most strikingly dissociated from other types of memory in amnesic patients who show priming despite damage to their temporal lobes that prevents them from forming new explicit memories (Gabrieli, Milberg, Keane, & Corkin, 1990; Hamann & Squire, 1997). Thus, priming is cognitively distinct from explicit memory, long-lasting, early developing, and depends on neural systems distinct from those serving explicit memory.

Because priming is automatic, effortless, unconscious, and neuroanatomically separate from sophisticated forms of memory such as episodic memory, researchers have theorized that it may be evolutionary old (Tulving, 1995). Additionally, a neural mechanism theorized to underlie priming, repetition suppression (Wiggs & Martin, 1998), has been observed in electrophysiological recordings in nonhuman primates (Mcmahon & Olson, 2007). This theory and evidence leads us to expect priming in monkeys.

It is therefore surprising that the only evidence of priming in nonhumans comes from pigeons (Brodbeck, 1997). Pigeons were trained to discriminate images of cats from images of cars and these images could be masked by placing small black boxes over a random 50% of the image. An irrelevant warning image preceded each trial. On study trials, the warning image was the S+ that would appear in the subsequent test trial. On test trials, the warning image was normal, but the S+ had been seen as the warning image in a previous trial. Pigeons showed facilitated discrimination when the S+ image had been seen as the warning image on a previous trial, and this facilitation was evident even when the previous study trial occurred long enough ago that the pigeon would be unlikely to recognize the primed image. Brodbeck (1997) concluded that this facilitation was probably implicit and likely a result of priming. Oddly, the pigeons' accuracy was also facilitated on study trials, which the author suggests might represent short-lived conceptual priming.

There is one published claim of visual priming in monkeys based on evidence that monkeys were slightly faster at making symmetrical/asymmetrical judgments if they had recently seen the target stimulus (Mcmahon & Olson, 2007). Although this does show that prior exposure facilitated processing of the stimuli, no evidence was provided to indicate that the memory effect was implicit or otherwise dissociable from recognition performance. Given the short delays used (mean = 1.9 seconds), it is likely the monkeys would have recognized the primes and, thus, this study does not provide evidence for implicit priming in monkeys.

The phenomenon of perceptual priming is also similar to, but distinct from, the concept of "specific searching image" in studies of insect predation by birds (Tinbergen, 1960). After repeated exposure to cryptic prey, such as when foraging for camouflaged moths, birds may form a mental image that facilitates subsequent searches for that prey. However, unlike the facilitation caused by perceptual priming, the facilitation caused by forming a search image is short lived (Langley, Riley, Bond, & Goel, 1996) and diminished by divided attention (Dukas & Kamil, 2001). This suggests that formation of a search image acts as a type of short-term attentional priming (Blough, 2001; Reid & Shettleworth, 1992; Shettleworth, 2010) rather than the long-term perceptual priming seen in humans.

We tested for priming in rhesus monkeys using procedures similar to those that have been effective in humans. As in priming studies in which humans were asked to name partially occluded images that they either had or had not seen previously (Mitchell, 2006; Snodgrass & Feenan, 1990), we required monkeys to classify partially occluded photographs that they either had or had not seen previously. Based on the similarity of this method to that used with humans, and the positive findings from pigeons (Brodbeck, 1997), we hypothesized that monkeys would show superior performance, either in accuracy or latency, for images they had previously seen compared to novel images. Had this been the case we would have needed to discriminate between true priming and contamination by memory processes supporting recognition. We would have conducted subsequent experiments to determine whether facilitation of classification occurred under conditions in which monkeys did not recognize the prime, which would indicate that priming is distinct from recognition and might suggest that the facilitation of classification occurred implicitly. But these further tests were not required because we found no evidence of facilitation of classification by previous exposure.

2. Experiment 1 – Initial results

2.1. Material and Methods

2.1.1 Subjects—We tested six adult male rhesus monkeys (*Macaca mulatta*; mean age at start of testing = 3.2 years). They were pair-housed, on a 12-hour light/dark cycle, received a full food ration daily, and had ad libitum access to water. All monkeys had prior experience with various cognitive tests using a touchscreen computer, including delayed matching-to-sample. Prior to this study, monkeys had learned to classify photographs as containing birds, fish, flowers, or people by touching one of four symbols. They all learned to a high-level of accuracy and transferred immediately to novel photographs without a significant decrement in accuracy (Paxton, Basile, Brown, and Hampton, submitted). During the course of this study, monkeys also participated in a variety of other cognitive tests, intermixed with the described experiments during a given day. During testing, monkeys were separated from their partners by a protected-contact divider that allowed the monkeys to see and groom each other, but not to access other individuals' testing rigs.

2.1.2 Apparatus—Subjects were tested six days a week in their home cages, using portable testing rigs controlled by Presentation testing software (Neurobehavioral Systems, Albany, CA). Each rig was equipped with a 15" color LCD touch-screen (3M, St. Paul, MN) running at a resolution of 1024×768, generic stereo speakers, and two automatic food dispensers (Med Associates Inc., St. Albans, VT) that dispensed into food cups beneath the screen. Food rewards were nutritionally complete, banana flavored pellets (Bio-Serv, Frenchtown, NJ), supplemented by miniature chocolate candies on a random 10% of correct trials. One testing rig was attached to the front of each monkey's cage and remained there for seven hours, allowing the monkeys to work at their own pace during the day.

2.1.3 Stimuli—Stimuli were color photographs (Figure 1 and Figure 2a) gathered from the online photo repository Flickr (Yahoo!, Sunnyvale, CA) using the batch downloading tool FlickrDown (<http://greggman.com>). Duplicates were eliminated using DupDetector (Prismatic Software, Anaheim, CA) and visual inspection, were shuffled randomly and renamed using 1-4a Rename (<http://www.1-4a.com>), and were cropped to 300×400 pixels using Adobe Photoshop (Adobe, San Jose, CA). Each photograph depicted birds, fish, flowers, or people. For each photograph, the target category was the dominant subject of the image and each image could not depict multiple categories. Otherwise, images varied widely in perceptual features (e.g., fish could be in schools or alone, goldfish or sharks, in the ocean or on a plate). Because the priming effect should be easiest to measure when comparing

previously-seen images to completely novel images, the size of the stimulus set was effectively unbounded, as novel images were added to the set each session.

2.1.4 Procedure—We ran one 100-trial session per day. Each session was preceded by presentation of primes. Monkeys saw each of 12 completely-novel images one at a time in the center of the screen and had to touch each one ten times (FR 10) to trigger presentation of the next image. We presented three images from each of the four categories in random order. One hundred classification trials immediately followed the 12 primes. To start a trial, monkeys touched a green box in the bottom center of the screen twice (FR 2). They then saw a single image in the center of the screen and touched it to bring up the four classification symbols. Touching the correct classification symbol resulted in food reward and positive audio feedback (“Woo-hoo!” or “Excellent!”). Touching one of the incorrect classification symbols resulted in a five-second time out, during which the screen was black, and negative audio feedback (“D’oh!”). Trials were separated by an unfilled three-second interval.

Of the 100 classification trials, the first four were always warm-up trials using familiar unmasked images. Of the remaining 96 classification trials, each block of eight trials contained two images from each of the four categories, and half of the images were covered with a black checkerboard mask. The checkerboard mask was composed of black boxes (40 pixels wide $\times$ 30 pixels tall; Figure 1 and Figure 2a) that obscured 50% of the image. The four unmasked images were always familiar. Of the four masked images in each block of eight trials, two were familiar, one was a primed image from the initial 12 trials at the start of the session, and one was an unprimed image that was completely novel. Within each block of eight trials, the order of the images, which four images were masked, and the placement of the primed and unprimed images was random. Within the session, the primes were presented in the reverse of the order in which they had initially been seen, allowing us to assess the priming effect at a relatively wide range of delays within a single session. We ran twenty-four sessions, resulting in 288 primed trials and 288 unprimed trials for each monkey. For each session of this experiment and all subsequent experiments, the 12 primed and 12 unprimed images were novel. The remaining set of familiar images was continually refreshed by incorporating the 24 previously-novel images from the previous day’s testing and eliminating the oldest 24 images.

2.1.5 Data analysis—For all experiments, accuracy was measured as the proportion of images correctly classified. All proportions were arcsine transformed prior to statistical analysis to better approximate normality (Aron & Aron, 1999). Latency was the median time from onset of the sample to selection of one of the symbols on correct trials only. Paired *t*-tests were used to compare performance on primed trials to that on unprimed trials, and one-sample *t*-tests were used to compare performance to chance levels. All statistical tests were two-tailed with $\alpha = .05$.

2.2 Results and Discussion

Monkeys were not more accurate at classifying primed images than unprimed images (Figure 3, left; $t_{(5)} = 0.6$, $p = .6$). Nor were they faster at correctly classifying primed images compared to unprimed images (Figure 3, right; $t_{(5)} = 0.1$, $p = .9$). It is unlikely that the lack of memory effect was due to classification accuracy being at a level where facilitation would be undetectable. Human subjects showed the largest priming effect when stimulus identification accuracy was roughly halfway between ceiling and floor levels, about 60% (Snodgrass & Feenan, 1990). The absolute classification accuracy of our monkeys was roughly in this range as well, with room for priming to improve performance. Overall, this

result surprised us, as the monkeys had seen the primed images unmasked at the start of the session, whereas they had never seen the unprimed images, masked or unmasked.

3. Experiment 2 – Immediate primes

In Experiment 1, we had hypothesized that we would observe a memory effect of having seen the primed images at the start of the session. However, we did not observe any memory effect at all. In Experiment 2, we attempted to increase memory for the primes by presenting them immediately before each primed trial, rather than at the beginning of the session. We hypothesized that reducing the delay between prime and classification of the masked primed image would increase memory for the prime and produce a memory effect.

3.1 Material and Methods

Subjects, apparatus, and stimuli were as described in Experiment 1 (see Figure 2a).

3.1.1 Procedure—Procedures were the same as in Experiment 1, with the exception that the initial 12 priming trials were interleaved with the classification trials, such that each prime was displayed immediately before the beginning of the trial on which the prime was to be classified. A three-second intertrial-interval separated primes and primed trials. Thus the minimum time from seeing the intact prime to classifying the masked version of the same image was approximately three seconds. Unprimed trials were preceded by other classification trials, as in Experiment 1.

3.2 Results

Monkeys were not more accurate at classifying primed images than unprimed images (Figure 4, left; $t_{(5)} = 1.2$, $p = .3$). Nor were they faster at correctly classifying primed images compared to unprimed images (Figure 4, right; $t_{(5)} = 1.2$, $p = .3$).

4. Experiment 3 – Black & white images

In Experiments 1 and 2, monkeys were no better at classifying recently-seen color photographs than at classifying completely novel color photographs. It is possible that this is because the monkeys were not classifying the photographs based on the shapes of the category exemplars depicted, but based on a simpler perceptual cue that correlated with category membership. In one classic study of classification by monkeys, for example, researchers attempted to train monkeys to classify color photographs based on the presence or absence of humans; however, the monkeys actually learned to classify based on the presence or absence of the color red, which happened to correlate with the presence or absence of humans (D'amato & Van Sant, 1988). In the current study, it seemed possible that our monkeys may also have learned a color discrimination; fish photos often had a blue background, humans photos usually contained flesh-tones, etc. In Experiment 3, we replaced the color photographs with black and white photographs. This tested whether monkeys were classifying images based on relatively simple color cues. Additionally, removing the color cues might increase the monkeys' attention to the shape of the category members depicted in each photograph. Human priming is thought to often be dependent on the shape of the primed image and our ability to perceptually close occluded parts of that shape (Snodgrass & Feenan, 1990; Wiggs & Martin, 1998), so the priming effect in monkeys might be most evident when monkeys attend less to color and more to shape. We hypothesized that eliminating color cues would encourage attention to shape and produce a memory effect of having seen the unmasked image prior to classification.

4.1 Material and Methods

Subjects, apparatus, and procedures were as described in Experiment 2.

4.1.1 Stimuli—Stimuli were as described in Experiment 2 with the exception that all photographs were fully desaturated using Adobe Photoshop (Adobe Systems Incorporated, San Jose, CA) to eliminate all color (see Figure 2b).

4.2 Results

Monkeys were able to correctly classify black and white photographs well above chance both when unmasked ($t_{(5)} = 26.0, p < .001$) and when masked ($t_{(5)} = 12.2, p < .001$). Monkeys showed a nonsignificant trend towards being more accurate at classifying primed images than unprimed images (Figure 5, left; $t_{(5)} = 2.4, p = .06$). They were not faster at correctly classifying primed images compared to unprimed images (Figure 5, right; $t_{(5)} = 1.0, p = .4$). Accurate discrimination of the black and white images indicates that the lack of a significant memory effect in the previous experiments was not due to the monkeys classifying the images based on color alone. However, if experience with black and white images resulted in increased attention to the shape of the category members, it did not produce significant priming.

5. Experiment 4 – Category repetition control

In Experiment 3, monkeys showed a nonsignificant trend towards being more accurate at classifying primed images compared to unprimed images. In Experiment 4, we evaluated whether this trend would replicate under more controlled conditions. In Experiments 2 and 3, the monkeys saw and touched an unmasked prime approximately three seconds before being required to categorize a masked version of the same image. In contrast, when monkeys classified masked unprimed images, the previous trial had been a normal classification trial. In Experiment 4, we introduced category control images immediately before the unprimed trials, in which the monkeys saw and touched an unmasked novel image from the same category as the upcoming unprimed image. These category control images controlled for any effect of increased attention or motivation caused by having the primed trial preceded by an image of the same category.

5.1 Material and Methods

Subjects, apparatus, and stimuli were as described in Experiment 3 (see Figure 2b).

5.1.1 Procedure—Procedures were the same as in Experiment 3 with the exception that the monkeys now had to touch a novel image prior to both primed and unprimed trials. Like the primes, these category control images were presented in the center of the screen, required ten touches, and were separated from the next trial by an ITI of three seconds. Category control images were always novel, unmasked images from the same category as the masked unprimed image that monkeys would classify on the subsequent trial, but unlike primes, were not the same image. We ran six sessions.

5.2 Results

Monkeys were not more accurate at classifying primed images than unprimed images (Figure 6, left; $t_{(5)} = 0.9, p = .4$). Nor were they faster at correctly classifying primed images compared to unprimed images (Figure 6, right; $t_{(5)} = 0.4, p = .7$). This suggests that the nonsignificant trend seen in Experiment 3 was statistical noise rather than an actual effect.

6. Experiment 5 – Blur mask

In Experiments 1 through 4, images were made more difficult to classify by overlaying a black checkerboard pattern (Figure 1). This introduced a regularity to the image that may have encouraged monkeys to classify them based on small patches of texture or small individual features rather than on the overall shape of the discriminanda. In Experiment 5, we masked images by blurring them rather than applying the checkerboard pattern. We hypothesized that the blur mask would encourage attention to shape and produce a memory effect of having seen the unmasked image.

6.1 Material and Methods

Subjects, apparatus, and stimuli were as described in Experiment 5 (see Figure 2c).

6.1.1 Procedure—Procedures were the same as in Experiment 5 with the exception that the checkerboard mask was changed to a blur mask. Blurred versions of each image were created using a Gaussian blur filter in Adobe Photoshop (Adobe Systems Incorporated, San Jose, CA). Blur strength was adjusted for each individual monkey prior to this experiment such that the blur mask brought overall classification accuracy down to approximately halfway between chance level and that monkey's maximum accuracy with unmasked images.

6.2 Results

Monkeys were significantly more accurate at classifying primed images than unprimed images (Figure 7, left; $t_{(5)} = 4.4$, $p < .01$, $d = 1.8$). However, they were not faster at correctly classifying primed images compared to unprimed images (Figure 7, right; $t_{(5)} = 0.5$, $p = .6$). Although the accuracy benefit seen with primed images was statistically significant, it should be interpreted with caution. It represents a relatively small absolute improvement (3.1%), and was the lone significant result of our study thus far. It is possible that this result is a Type I error. We investigated this possibility in Experiment 6 by attempting to reproduce the result.

7. Experiment 6 – Depth of processing

In Experiments 1 through 5, monkeys were required to touch the primes ten times to indicate that they had seen them. However, it is possible that monkeys were ignoring these images, perhaps touching the center of the screen without actually looking at the image. In Experiment 6, we ensured that monkeys attended to the primes and category control images by requiring them to classify those images in the same manner as with normal unmasked classification trials. We hypothesized that requiring the monkeys to attend to and process the primes would strengthen the small memory effect found in Experiment 5.

7.1 Material and Methods

Subjects, apparatus, and stimuli were as described in Experiment 5 (see Figure 2c).

7.1.1 Procedure—Procedures were the same as in Experiment 5 with the exception that we now required monkeys to classify image primes and category control images, as described for normal trials, instead of merely touching them.

7.2 Results

Monkeys accurately classified the unmasked primes at levels significantly above chance (Figure 8, far left; $t_{(5)} = 40.2$, $p < .001$). However, monkeys were not more accurate at classifying primed images than unprimed images (Figure 8, left; $t_{(5)} = 0.7$, $p = .5$). Nor were

they faster at correctly classifying primed images compared to unprimed images (Figure 8, right; $t_{(5)} = 0.4$, $p = .7$). These results indicate that the monkeys were indeed attending to the primes, and that they had processed the primes enough to accurately classify them, but that this processing had no effect when classifying a masked version of the same image three seconds later. These results fail to replicate the memory effect observed in Experiment 5 under conditions in which the effect should have been strengthened, suggesting that the effect seen in Experiment 5 was a Type I error.

8. Experiment 7 – Line drawings

In Experiments 1 through 6, monkeys classified photographs. However, the majority of priming studies in humans use line drawings (Mitchell, 2006; Mitchell & Brown, 1988; Snodgrass & Feenan, 1990) or words (Hamann & Squire, 1997; Tulving et al., 1982), which are also composed of lines. To better match the conditions under which comparable priming experiments have been done in humans, we replaced the photographs with line drawings. Removing most color and texture cues might also increase the monkeys' attention to the shape of the category members depicted in each image. We hypothesized that using line drawings would produce a memory effect of having seen the unmasked line drawing.

8.1 Material and Methods

Subjects and apparatus were as described in Experiment 6.

8.1.1 Stimuli—Stimuli were as described in Experiment 6 with the exception that all photographs were digitally transformed into line drawings (see Figure 2d) using Adobe Photoshop (Adobe Systems Incorporated, San Jose, CA). The final result looked like detailed versions of the classic Snodgrass figures (Snodgrass & Corwin, 1988) that have been used successfully in several studies of human priming (Snodgrass & Feenan, 1990).

8.1.2 Procedure—Procedures were the same as in Experiment 6 with the exception that we used a white checkerboard mask similar to that used in Experiments 1 through 4. Because the stimuli consisted of black line drawings on white backgrounds, the white checkerboard mask was effectively invisible on certain areas of each picture, reducing the grid-like nature of the black checkerboard mask (see Figure 2d).

8.2 Results

Monkeys accurately classified the unmasked primes at levels significantly above chance (Figure 9, far left; $t_{(5)} = 34.1$, $p < .001$). Transfer of classification performance to line drawings indicates that the monkeys were not classifying images based on texture or grayscale cues alone, and were likely classifying based on global shape. However, monkeys were not more accurate at classifying primed images than unprimed images (Figure 9, left; $t_{(5)} = 0.3$, $p = .8$). Nor were they faster at correctly classifying primed images compared to unprimed images (Figure 9, right; $t_{(5)} = 2.2$, $p = .1$). Using line drawings did not produce any memory effect.

9. Experiment 8 – Increased prime exposure

In Experiments 6 and 7, we required monkeys to classify the unmasked prime before classifying a masked version of the same image. Surprisingly, this additional processing did not improve subsequent classification. In Experiment 8, we took this reasoning to its logical extreme and required monkeys to classify each unmasked prime ten times in a single session before classifying the masked version of the image. In humans, the size of the priming effect increases with repetition of the prime (Wiggs, Martin, & Sunderland, 1997). Consequently,

we hypothesized that repeating each unmasked prime ten times would facilitate subsequent classification of the masked primed image.

9.1 Material and Methods

Subjects, apparatus, and stimuli were as described in Experiment 7 (see Figure 2d).

9.1.1 Procedure—Each session consisted of two phases. The first half of the session consisted of 120 trials in which monkeys classified 12 novel, unmasked primes 10 times each. Primes were pseudorandomized such that each block of 12 trials contained each prime image in a random order. The second half of the session consisted of 24 trials in which monkeys classified the 12 masked primes and 12 completely novel, masked unprimed images. The order of primed and unprimed trials was pseudorandomized such that each block of four trials consisted of two primed and two unprimed trials in random order. Ten sessions were run, resulting in 120 masked primed images and 120 masked unprimed images.

9.2 Results

Monkeys were not more accurate at classifying primed images than unprimed images (Figure 10, left; $t_{(5)} = 0.7$, $p = .5$). Nor were they faster at correctly classifying primed images compared to unprimed images (Figure 10, right; $t_{(5)} = 0.9$, $p = .4$). Surprisingly, classifying an unmasked image 10 times did not improve subsequent classification of a masked version of that same image.

11. Experiment 9 – Shuffled classification

In Experiments 7 and 8, monkeys classified line drawings, suggesting that they were not classifying images based on color or texture alone. However, it is still possible that monkeys classified images based on very small features, such as the sharp angle formed by a bird's beak or the rounded line formed by a person's eye. Priming in humans is thought to rely on the shape of the primed image and on perceptual closure, our tendency to mentally fill-in occluded areas of an image (Snodgrass & Feenan, 1990; Wiggs & Martin, 1998); therefore, monkeys may not show priming if they classify images based on hyper-local cues. Indeed, memory for a whole intact image may not help subsequent masked classification at all if that masked classification is based on the presence or absence of a small, specific feature. In Experiment 9, we tested whether monkeys were classifying masked images based on the overall shape of the target or on small, hyper-local features by shuffling the visible sections of the masked image (similar to Aust & Huber, 2001). If monkeys perceive the masked image as an occluded whole, then the position of the un-occluded sections should matter and shuffling them should reduce accuracy. In contrast, if monkeys focus on small, relatively simple features, then performance should be unaffected because the small features are still present and intact when the un-occluded sections are shuffled.

11.1 Materials and methods

Subjects, apparatus, and stimuli were as described in Experiments 7 and 8 (see Figure 2e).

11.1.1 Procedure—Each session consisted of two phases. In phase 1, monkeys classified 24 warm-up images, consisting of unmasked line drawings. In phase 2, monkeys classified unmasked line drawing images, masked line drawing images, and masked line drawing images in which the visible segments were shuffled. The visible segments were randomly shuffled with the restrictions that they must remain upright, could not remain in the same location, could not occupy an area that was masked, and must remain the same distance from the center of the image. In this way, small features and their distance from the center of

the image were preserved, but the arrangement of those features relative to one another was disrupted. That is, local features were preserved but global structure was disrupted. Each block of eight trials contained four unmasked trials, two intact masked trials, and two scrambled masked trials. One session of 424 trials was run, providing 24 warm-up, 200 unmasked, 100 intact masked, and 100 scrambled masked trials. The same 100 images were used in the intact masked and scrambled masked trials, with half the images seen first intact and half seen first as scrambled. Thus, both intact masked images and scrambled masked images contained identical features that differed only in their arrangement (see Figure 2e).

11.2 Results

Scrambling the masked images significantly decreased classification accuracy compared to intact masked images (Figure 11; $t_{(5)} = 5.2$, $p < .01$, $d = 2.1$). This suggests that monkeys were not classifying images based on small, hyper-local features alone, and that this cannot explain the lack of a memory effect observed in previous experiments. This result is consistent with the idea that monkeys, like humans, perceptually close missing gaps in the image, and with previous findings that monkeys perceive lines as continuing through gaps (Feltner & Kiorpes, 2010) and behind occluding objects (Fujita, 2001).

12. Experiment 10 – Recognition of primes

In Experiments 2, 6, and 8, we attempted to ensure that monkeys remembered the prime image by moving it closer to the primed test, by having them classify it, and by having them classify it ten times. In Experiment 10, we assessed whether monkeys actually did remember the primes by intermixing recognition trials with the normal classification, primed, and unprimed trials. We tested recognition for both unmasked and masked versions of the novel primes at the same memory interval as between primes and primed trials. Based on previous studies in which our monkeys remembered various types of stimuli over similar memory delays (Basile & Hampton, 2010, 2011), we hypothesized that monkeys would recognize the primes.

12.1 Materials and method

Subjects, apparatus, and stimuli were as described in Experiment 2 (see Figure 2a).

12.1.1 Procedure—Procedures were the same as in Experiment 6 with the exception that some primed trials were replaced by two-choice recognition tests. In a recognition test, monkeys first touched a green start box to initiate the trial, and then saw two images, one on the left center of the screen and one on the right center of the screen. One of the recognition images was the primed image from the preceding trial and the other image was a novel distractor from the same category. The correct screen location was pseudorandomized and balanced such that the primed image was presented on each side twice randomly within each block of four trials. On some recognition trials, the two options were both masked by the black checkerboard mask as in Experiments 1 through 4. Touching the primed image resulted in food reward and positive audio feedback (“Woo-hoo!” or “Excellent!”). Touching the novel image resulted in a five-second time out, during which the screen was black, and negative audio feedback (“D’oh!”). Trials were separated by an unfilled three-second interval. This general procedure was familiar to the monkeys, but they had never done matching with these stimuli or intermixed with classification trials.

Each session consisted of 172 trials: 4 unmasked warm-up images, 12 masked familiar images, 12 unmasked familiar images, 48 unmasked primes, 24 masked primed, 24 recognition, 24 unmasked category control images, and 24 masked unprimed images. We ran five sessions with the recognition images unmasked and five sessions with the

recognition images masked. This resulted in a total of 240 primed, 240 unprimed, 120 unmasked recognition, and 120 masked recognition trials.

12.2 Results

Monkeys accurately classified the unmasked primes at levels significantly above chance ($t_{(5)} = 34.7, p < .001$). However, monkeys were not more accurate at classifying primed images than unprimed images (Figure 12, left; $t_{(5)} = 0.4, p = .7$). Nor were they faster at correctly classifying primed images compared to unprimed images ($t_{(5)} = 0.1, p = .9$). In contrast, monkeys did recognize the primed images significantly above chance both when unmasked and when masked (Figure 12, right; unmasked: $t_{(5)} = 4.7, p < .01, d = 1.9$; masked: $t_{(5)} = 4.4, p < .01, d = 1.8$). These results indicate that the monkeys did remember the primed images at the time they were classifying the masked version of those images, but that remembering the image did not facilitate classification.

13. Experiment 11a – Attempted replication of pigeon procedures

We designed Experiments 1 through 10 based on studies of priming in humans. However, the only positive evidence of priming in nonhumans comes from a study of pigeons (Brodbeck, 1997). In Experiment 11a we attempted to replicate the methods used with pigeons as closely as possible. We hypothesized that monkeys would show a priming effect similar to what has been observed with pigeons.

13.1 Materials and methods

Subjects and apparatus were the same as in Experiments 1 through 10.

13.1.1 Stimuli—Stimuli were 80 color photographs each of cats, cars, or still-life images that contained neither cats nor cars. Half of each type of photo was used in training, and the other half was used for transfer and testing. All photos were gathered from the online photo repository Flickr (Yahoo!, Sunnyvale, CA) using the batch downloading tool FlickrDown (<http://greggman.com>). Duplicates were eliminated using DupDetector (Prismatic Software, Anaheim, CA) and visual inspection, were shuffled randomly and renamed using 1-4a Rename (<http://www.1-4a.com>), and were cropped to 400×400 pixels using Adobe Photoshop (Adobe, San Jose, CA). For each photograph, the target category was the dominant subject of the image and each image could not depict multiple categories. Otherwise, images varied widely in perceptual features (e.g., cats could be alone or in groups, outdoors or inside, running or sleeping).

13.1.2 Procedure—Procedures were closely based on those used successfully with pigeons (Brodbeck, 1997) except where noted.

Testing consisted of four phases. In phase 1, monkeys learned an S+/S− discrimination. On each trial, one cat and one car were presented on the center left and center right of the screen. The location of the S+ was balanced and pseudorandomized such that the S+ was presented twice on each side of the screen randomly within each block of four trials. If the monkey touched the S+ image, he received a food reward and a positive audio reinforcer (“woo-hoo!” or “excellent!”). If the monkey touched the S−, he received a negative audio reinforcer (“d’oh!”). All trials were separated by a 30-second ITI during which the screen was black. The S+ category was counterbalanced across monkeys such that cats were S+ for three monkeys and S− for the other three monkeys. Forty images were used from each category. One 200-trial session was run per day, for three days. This phase differs from that used with the pigeons in that stimuli were presented with a touchscreen rather than a slide

projector, and that the 600 total trials were run in three sessions of 200 trials rather than 15 sessions of 40 trials.

In phase 2, we introduced a warning stimulus that monkeys had to touch to proceed to the discrimination. The warning stimuli were 40 still-life color photographs that contained neither cats nor cars. On each trial, one warning stimulus was presented in the center of the screen, monkeys touched it 20 times to proceed, the warning stimulus was replaced by a black screen for 200msec, and then the discrimination trial proceeded as described in phase 1. One 200-trial session was run. This phase differed from that used with pigeons in that the 200 trials were presented in one session rather than five sessions of 40 trials.

In phase 3, we assessed whether monkeys had learned the category discrimination by transferring them to 40 novel cat, 40 novel car, and 40 novel warning images. All other procedures were the same as in phase 2. This phase differed from that used with pigeons in that the 200 trials were presented in one session rather than five sessions of 40 trials.

In phase 4, we assessed how much of the photographs would need to be occluded by the mask to produce an accuracy level near to that of the pigeons. Mask titration was necessary because we expected monkeys' classification accuracy to be much better than that of pigeons, and because priming would not be observable if accuracy was at ceiling level. Discrimination images were masked by randomly placing a number of black boxes (50×50 pixels) over each image (see Figure 2f). Individual trials varied in how many blocks were placed, occluding 50%, 60%, 70%, or 80% of the image. One session of 200 trials was run, with 25 trials with each occlusion level. This phase was not present in the pigeon study; however, masks were constructed as described with the pigeons with the exception that they were made of pixels rather than electrical tape. In phase 4, we tested for priming by sometimes replacing the warning stimulus with the S+ stimulus that would be seen on the subsequent trial. We ran three types of trials. On control trials, the warning stimulus and discrimination were presented as described in phase 3. On study trials, the warning stimulus was replaced with the S+ that would be seen on the subsequent trials. On test trials, the S+ was the warning stimulus from the previous trial. For example, on trial n , the warning stimulus might be cat#2 and the discrimination could be cat#1 versus car #1; then on trial $n + 1$, the warning stimulus might be a house and the discrimination could be car#2 versus cat#2. All discrimination images were masked at the level determined by phase 3; the warning stimuli were always unmasked. Each session contained 200 trials: 100 control, 50 study, and 50 test. Four sessions were run. This phase differed from that used with pigeons in that we ran four sessions of 200 trials rather than 16 sessions of 40 trials.

13.2 Results

Monkeys learned the cats/cars discrimination to over 80% accuracy by the end of the first training session and 98% accuracy by the final training session. They were 98% correct when transferring to novel stimuli. Monkeys required the highest mask level, which occluded 80% of the image and brought performance down to 81% during phase 3. In phase 4, monkeys were not more accurate at discriminating primed images on test trials than they were at discriminating unprimed images on control trials (Figure 13, left; $t_{(5)} = 0.7$, $p = .4$). Nor were they faster at correctly discriminating the primed images than the unprimed images (Figure 13, right; $t_{(5)} = 1.5$, $p = .2$). Under conditions similar to those in which pigeons showed a memory effect of having recently seen the to-be-classified stimuli (Brodbeck, 1997), monkeys did not.

14. Experiment 11b – Replication of 11a with species-relevant categories

In Experiment 11a, we attempted to reproduce the positive evidence of priming in pigeons (Brodbeck, 1997) using methods and stimuli that were as similar as possible. However, under these similar conditions, monkeys did not behave like pigeons. In Experiment 11b, we re-ran Experiment 11a with new stimuli. Instead of cats and cars, monkeys had to discriminate color photographs of adult male rhesus monkeys from photographs of adult female rhesus monkeys. These stimuli might produce a memory effect because overall discrimination performance should be further way from ceiling levels, as male and female monkeys are more perceptually similar than cats and cars, or because monkeys' perceptual systems may have evolved under pressures to process natural stimuli, such as fellow monkeys while obscured behind other objects. We hypothesized that monkeys would show a priming effect similar to what has been observed with pigeons.

14.1 Materials and methods

Subjects, apparatus, and procedures were the same as in Experiment 11.

14.1.1 Stimuli—Stimuli were 80 color photographs each of adult male rhesus monkeys, adult female rhesus monkeys, or still-life images that did not contain monkeys (see Figure 2g).

14.2 Results

Monkeys learned the male/female discrimination to over 91% accuracy by the final training session and were 89% correct when transferring to novel stimuli, which included novel photographs of the same individuals and novel photographs of novel individuals. Monkeys required the highest or second-highest mask level, which occluded 80% or 70% of the image and brought performance down to an average of 72% during phase 3. In phase 4, monkeys were not more accurate at discriminating primed images on test trials than they were at discriminating unprimed images on control trials (Figure 14, left; $t_{(5)} = 2.0$, $p = .1$). Nor were they faster at correctly discriminating the primed images than the unprimed images (Figure 14, right; $t_{(5)} = 1.5$, $p = .2$). Using a paradigm similar to one that provided positive evidence of priming with pigeons (Brodbeck, 1997), and stimuli that should be ecologically relevant to monkeys, monkeys showed no benefit of having recently seen a to-be-classified image.

15. General discussion

Across 11 experiments, monkeys did not show priming, nor did they show any reliable benefit of having seen to-be-classified images. Our results clearly show that the monkeys attended to the primes, processed them enough to classify them accurately, and remembered them at the time they were classified for the second time. It is surprising that remembering images to a degree sufficient to support accurate recognition did not help monkeys classify them.

It is unlikely that our results were due to the monkeys classifying images based on relatively simple cues. Monkeys could not have learned specific responses to individual images, because they transferred classification performance to novel images without performance decrement (Paxton, Basile, Brown, and Hampton, submitted) and continued to accurately classify novel images throughout all experiments. Nor were monkeys classifying images based on relatively simple cues, such as color or texture, as the exemplars within each category varied widely in their perceptual features and monkeys continued to accurately classify images when in color, in black and white, line drawings, occluded by black squares,

occluded by white squares, or blurred. Finally, monkeys were not classifying images based on small, hyper-local features alone, as shuffling the visible features significantly reduced accuracy. Together, these results indicate that the monkeys classified images based on global form, a process that would be expected to be facilitated by memory of the image.

Our null results are unlikely to be the product of low statistical power. First, it is unlikely that the size of our subject pool masked detection of priming. Priming is often seen in case studies of single human subjects (Gabrieli et al., 1990; Hamann & Squire, 1997), and the positive evidence from pigeons comes from a study using fewer subjects than the current experiment (Brodbeck, 1997). Second, it is unlikely that our measures were overly-noisy or that there were insufficient opportunities to observe priming. Each experiment used a large number of trials, which reduced measurement noise for each subject, and we conducted a large number of experiments, which provided many opportunities to observe priming. Third, our methods were sufficient to detect memory for the primes, as we were able to detect significant recognition in Experiment 10. Together, this suggests we would have detected an effect if one had been present.

We failed to replicate the findings of the single study of priming in nonhumans (Brodbeck, 1997). This apparent inconsistency has several potential explanations. First, priming may be a type of memory present in humans and pigeons, but not in monkeys; however, this seems phylogenetically unlikely.

Second, priming could be a type of memory unique to humans, and the positive results seen in pigeons may be the result of some other process that is present in pigeons but not monkeys, or some process that was recruited by Brodbeck's (1997) procedures but not ours. Pigeons have repeatedly failed to show evidence that they perceptually complete occluded figures (Fujita & Ushitani, 2005; Sekuler, Lee, & Shettleworth, 1996; Ushitani & Fujita, 2005; Ushitani, Fujita, & Yamanaka, 2001), and manipulations that should affect classification based on global shape, such as scrambling the image, often do not impair classification in pigeons (Aust & Huber, 2001). Thus, it appears that unlike our monkeys, pigeons are more likely to process local rather than global features in classifications tasks. If monkeys and pigeons classify visual images using different processes, this may account for the difference in results. We are aware of only one other attempt to replicate Brodbeck (1997), and that work also failed to find priming in pigeons (S.L. Astley, personal communication, March, 30, 2010). More published data, especially from pigeons, are clearly needed to properly evaluate the possibility that evidence of priming in pigeons is due to some other process.

Third, priming could be a type of memory shared among humans, monkeys, and pigeons, but the current study was not designed appropriately to detect it. Although we based our methods on studies that have showed positive evidence of priming in humans and pigeons, and we explored a large number of reasonable manipulations, it is possible we failed to identify the critical conditions under which we would find priming, or indeed any memory effect on classification, in monkeys. This seems likely, based on the strong theoretical case that priming should be phylogenetically widespread (Tulving, 1995) and the strong mechanistic case that the likely neural underpinnings of priming have been observed in monkeys (Wiggs & Martin, 1998). Evidence of priming in monkeys may yet emerge from studies using different techniques, such as presenting primes extremely rapidly (Bar & Biederman, 1998) or measuring performance on primed images that are not degraded (Mitchell & Brown, 1988).

Whether or not monkey memory systems include a system for perceptual priming, our suite of findings indicates a dissociation. Experiment 10 showed that monkeys remembered the

primes sufficiently to recognize them while simultaneously showing no facilitation of classification. This suggests that the visual processing necessary for recognition is cognitively encapsulated from that necessary for classification. It may be of interest to conduct further studies to better characterize the nature of this dissociation of visual memory and visual classification. For now, recognition without priming in monkeys presents a puzzle.

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Highlights for Monkeys show recognition without priming in a classification task by Benjamin M. Basile and Robert R. Hampton

- Visual priming should be widespread but evidence exists only in humans and pigeons
- Monkeys showed no evidence of perceptual priming across several manipulations
- We duplicated procedures used with pigeons but still found no evidence of priming
- Monkeys recognized the primes in matching-to-sample probe trials
- Recognition without priming under matched conditions presents a puzzle

Figure 1.

Diagram of a prime (left), and primed and unprimed classification trials (right). For primes at the beginning of the session, monkeys saw and touched (FR=10) a novel, unmasked photograph. On classification trials, monkeys touched a green start box (FR=2) to initiate the trial, saw and touched (FR=2) a masked sample image, and finally classified the masked image by touching (FR=2) one of the four colored symbols. The symbols used were: red triangle = birds, yellow star = fish, blue plus = people, green circle = flowers. On primed trials, the to-be-classified image had been seen once as one of the primes. On unprimed trials, the to-be-classified image was completely novel.

Figure 2.

Examples of stimuli used in Experiments 1-11. A) Color photographs with black checkerboard masks, as used in Experiments 1, 2, and 10. B) Black & white photographs with black checkerboard masks, as used in Experiments 3 and 4. C) Black & white photographs with blur masks, as used in Experiments 5 and 6. D) Line drawings with white checkerboard masks, as used in Experiments 7 and 8. E) Line drawings with a white checkerboard mask in which the arrangement of un-occluded elements was either left intact or scrambled, as used in Experiment 9. F) Color photographs of cats or cars with black masks composed of randomly-placed black squares, as used in Experiment 11a. G) Color photographs of male or female rhesus monkeys with black masks composed of randomly-placed black squares, as used in Experiment 11b. For A-E, the same photograph is depicted to emphasize the various manipulations; however, primed and unprimed images were always novel for each experiment.

Figure 3.

Classification accuracy and response latency for primed and unprimed images in Experiment 1. Left two bars: mean proportion ($\pm$ SEM) of masked primed and unprimed images correctly classified. The dashed line represents the proportion correct that would be expected by chance. Right two bars: group mean of the individual median response latencies to correctly classify primed and unprimed images.

Figure 4.

Classification accuracy and response latency for primed and unprimed images in Experiment 2. Left two bars: mean proportion ($\pm$ SEM) of masked primed and unprimed images correctly classified. The dashed line represents the proportion correct that would be expected by chance. Right two bars: group mean of the individual median response latencies to correctly classify primed and unprimed images.

Figure 5.

Classification accuracy and response latency for primed and unprimed images in Experiment 3. Left two bars: mean proportion ($\pm$ SEM) of masked primed and unprimed images correctly classified. The dashed line represents the proportion correct that would be expected by chance. Right two bars: group mean of the individual median response latencies to correctly classify primed and unprimed images.

Figure 6.

Classification accuracy and response latency for primed and unprimed images in Experiment 4. Left two bars: mean proportion ($\pm$ SEM) of masked primed and unprimed images correctly classified. The dashed line represents the proportion correct that would be expected by chance. Right two bars: group mean of the individual median response latencies to correctly classify primed and unprimed images.

Figure 7.

Classification accuracy and response latency for primed and unprimed images in Experiment 5. Left two bars: mean proportion ($\pm$ SEM) of masked primed and unprimed images correctly classified. The dashed line represents the proportion correct that would be expected by chance. Right two bars: group mean of the individual median response latencies to correctly classify primed and unprimed images.

Figure 8.

Classification accuracy and response latency for primes, primed images, and unprimed images in Experiment 6. Left three bars: mean proportion ($\pm$ SEM) of unmasked primes, masked primed images, and masked unprimed images correctly classified. The dashed line represents the proportion correct that would be expected by chance. Right two bars: group mean of the individual median response latencies to correctly classify primed and unprimed images.

Figure 9.

Classification accuracy and response latency for primes, primed images, and unprimed images in Experiment 7. Left three bars: mean proportion ($\pm$ SEM) of unmasked primes, masked primed images, and masked unprimed images correctly classified. The dashed line represents the proportion correct that would be expected by chance. Right two bars: group mean of the individual median response latencies to correctly classify primed and unprimed images.

Figure 10.

Classification accuracy and response latency for primed and unprimed images in Experiment 8. Left two bars: mean proportion ($\pm$ SEM) of masked primed and unprimed images correctly classified. The dashed line represents the proportion correct that would be expected by chance. Right two bars: group mean of the individual median response latencies to correctly classify primed and unprimed images.

Figure 11. Classification accuracy for masked images that were intact or scrambled in Experiment 9. Bars depict mean proportion correct ($\pm$ SEM). The dashed line represents the proportion correct that would be expected by chance.

Figure 12.

Classification and recognition accuracy for primed and unprimed images in Experiment 10. Left two bars: mean proportion ($\pm$ SEM) of masked primed and masked unprimed images correctly classified. Right two bars: mean proportion ($\pm$ SEM) of unmasked primes and masked primes correctly recognized. The dashed line represents the proportion correct that would be expected by chance. Asterisks mark recognition accuracy that is significantly higher than chance.

Figure 13.

Classification accuracy and response latency for primed and unprimed images in Experiment 11a. Left two bars: mean proportion ($\pm$ SEM) of masked primed and unprimed images correctly classified. The dashed line represents the proportion correct that would be expected by chance. Right two bars: group mean of the individual median response latencies to correctly classify primed and unprimed images.

Figure 14.

Classification accuracy and response latency for primed and unprimed images in Experiment 11b. Left two bars: mean proportion ($\pm$ SEM) of masked primed and unprimed images correctly classified. The dashed line represents the proportion correct that would be expected by chance. Right two bars: group mean of the individual median response latencies to correctly classify primed and unprimed images.