Recognition Memory in Marmoset and Macaque Monkeys: A Comparison of Active Vision

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Abstract

■ The core functional organization of the primate brain is remarkably conserved across the order, but behavioral differences evident between species likely reflect derived modifications in the underlying neural processes. Here, we performed the first study to directly compare visual recognition memory in two primate species—rhesus macaques and marmoset monkeys—on the same visual preferential looking task as a first step toward identifying similarities and differences in this cognitive process across the primate phylogeny. Preferences in looking behavior on the task were broadly similar between the species, with greater looking times for novel images compared with repeated images as well as a similarly strong preference for faces compared with other categories. Unexpectedly, we found large behavioral differences among the two species in looking behavior independent of image familiarity. Marmosets exhibited longer looking times, with greater variability compared with macaques, regardless of image content or familiarity. Perhaps most strikingly, marmosets shifted their gaze across the images more quickly, suggesting a different behavioral strategy when viewing images. Although such differences limit the comparison of recognition memory across these closely related species, they point to interesting differences in the mechanisms underlying active vision that have significant implications for future neurobiological investigations with these two nonhuman primate species. Elucidating whether these patterns are reflective of species or broader phylogenetic differences (e.g., between New World and Old World monkeys) necessitates a broader sample of primate taxa from across the Order. ■

INTRODUCTION

Like all closely related species, primates are distinguished from other taxonomic groups by a unique assemblage of phenotypic characteristics, such as their behavioral repertoire. However, even within the taxa, meaningful differences in each species behavioral repertoire emerged over the course of their adaptive radiation. Although many other taxonomic groups exhibit a notable range of sophisticated cognitive behaviors (Bugnyar, 2013; Heinrich, 2011; Finn, Tregenza, & Norman, 2009; Marino et al., 2007), the breadth of primate cognition and its intersection with key sensory processes is routinely emphasized as among the most idiosyncratic characteristics of the Order (Miller et al., 2016; Platt, Seyfarth, & Cheney, 2016; Koops, Visalberghi, & van Schaik, 2014; Rosati, Santos, & Hare, 2010; Burkart, Hrdy, & van Schaik, 2009; Whiten et al., 1999; Tomasello & Call, 1997). Unlike most mammals, primates rely almost entirely on vision and audition to build representations of the sensory world (Kaas, 2010, 2013; Allman, 1977). For example, our capacity to rapidly visually distinguish between items in the world that are familiar and those that are novel is characteristic of primate memory (Eichenbaum, Yonelinas, & Ranganath, 2007), but there has been little effort to directly compare these processes between species in the Order. Systematic comparisons of key cognitive processes in primate behaviors offer a powerful opportunity to identify shared and idiosyncratic characteristics which, in turn, can inform predictions about differences in the supporting neural mechanisms (Yartsev, 2017; Brenowitz & Zakon, 2015; Mitchell & Leopold, 2015).

Primate neuroscience has been dominated by studies of rhesus macaques—an Old World monkey—for several decades; however, common marmosets—a New World monkey—have more recently emerged as a powerful complementary model organism (Miller, 2017; Miller et al., 2016; Okano et al., 2016; Kishi, Sato, Sasaki, & Okano, 2014). Although these species share many of the core-defining characteristics of primate brains and behavior, notable differences are also evident. Not only are marmosets significantly smaller in body and brain size, but they are also, in contrast to macaques, entirely arboreal, endemic only to the forests of South America (Schiel & Souto, 2017). The marmoset behavioral repertoire also differs from macaques in a number of notable ways. Like humans, marmosets are among only a handful

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of primates that pair-bond (Fischer, 1993) and cooperatively care for their young (French, 1997; Solomon & French, 1997). These cooperative tendencies extend to other contexts, including food sharing (Brügger, Kappeler-Schmalzriedt, & Burkart, 2018), that are rare in other primates but, at the same time, consistent with the species' prosocial tendencies thought to be integral to marmoset cognitive evolution (Burkart & van Schaik, 2010; Burkart et al., 2009). Furthermore, marmosets are the only species of monkey for which there is experimental evidence of imitation in adults (Voelkl & Huber, 2000, 2007; Bugnyar & Huber, 1997), a unique social learning mechanism commonly employed in humans. Such differences may not be surprising, given that New World and Old World monkeys diverged from the human lineage ~35 and 25 mya, respectively. Although these simian groups are more closely related to each other than either is to humans (Springer, Meredith, Janecka, & Murphy, 2011), sufficient time has occurred for each species to adapt their behavioral repertoire to their respective niches while still relying on the shared primate functional brain architecture (Hung et al., 2015b; Mitchell & Leopold, 2015; Solomon & Rosa, 2014; Chaplin, Yu, Soares, Gattass, & Rosa, 2013). Importantly, we expect any observed differences to be placed within the context of copious similarities owing to their shared evolutionary history as primates, particularly for core cognitive systems inherent to primate behaviors, such as recognition memory.

Here, we utilized a visual preferential looking task (VPLT) from previous studies of visual recognition memory in both macaques and humans (Jutras & Buffalo, 2010; Crutcher et al., 2009; Wilson & Goldman-Rakic, 1984) to directly compare visual recognition memory in these two closely related primate species. Whereas a previous comparative study showed broadly similar patterns of visual behavior across these species (Mitchell, Reynolds, & Miller, 2014), more detailed approaches are needed to better characterize a broader range of cognitive processes. By testing subjects in each species on an identical task with identical visual images, we were able to directly compare several dimensions of each species' respective behavior—ranging from performance on the task to the fine details of eye movements—to identify points of similarity and important differences across these closely related primate species.

METHODS

Subjects and Surgery

Three adult common marmosets (*Callithrix jacchus*) A, K, and L and three adult rhesus macaques (*Macaca mulatta*) I, P, and T served as subjects to measure recognition memory based on preferential looking. All experiments were approved by the Institutional Animal Care and Use Committees at their respective institutions (A, K, and L at the University of California, San Diego, and I, P, and T at the University of Washington, Seattle). Surgical procedures for marmosets were as in Nummela, Jovanovic, de la Mothe, and Miller (2017) and Nummela, Coop, et al. (2017) with the following modifications: Nylon screws were used to anchor the head post, and C&M Metabond was not applied. Surgical procedures for macaques were as in Jutras and Buffalo (2010).

Behavioral Tasks

Rhesus macaques were tested on the VPLT while head-restrained and seated in a primate chair. The monkey initiated each trial by fixating on a white cross (the fixation target, 1°) at the center of the computer screen. After maintaining fixation on this target for 1 sec, the target disappeared and a square picture stimulus subtending 11° was presented. All stimuli were obtained from Flickr. A total of 3000 stimuli were used in this study, each only presented twice (a novel presentation and a repeat presentation). Each stimulus disappeared when the monkey's direction of gaze moved off the stimulus or after a maximum looking time of 5 sec. A blank screen was displayed for 1 sec between trials. The VPLT was given in 51 daily blocks of 6, 8, or 10 trials each, chosen pseudorandomly, for a total of 400 trials each day. The first half of each block was novel trials, in which an image that the subject had never viewed was presented. The second half of each block consisted of repeat trials, in which the images from the novel trials were shuffled and then presented again. The median delay between successive presentations was 8.1 sec. Reward was not delivered during blocks of the VPLT; however, five trials of the calibration task were presented between each block to give the monkey a chance to earn some reward and to verify calibration. The number of trials in each VPLT block was varied to prevent subjects from knowing when to expect the rewarded calibration trials.

For macaques, behavior was collected in a dimly illuminated room, 60 cm from a 19-in. CRT monitor. Eye movements were recorded using a noninvasive infrared eye-tracking system (ISCAN). Stimuli were presented using experimental control software (CORTEX, www.cortex.salk.edu). At the beginning of each recording session, the monkey performed a calibration task, which involved holding a touch-sensitive bar while fixating on a small (0.3°) gray point, presented on a dark background at various locations on the monitor. The monkey had to maintain fixation within a 3° window until the fixation point changed to an equiluminant yellow at a randomly chosen time between 500 and 1100 msec after fixation onset. The subject was required to release the touch-sensitive bar within 500 msec of the color change for delivery of a drop of applesauce. During this task, the gain and offset of the oculomotor signals were adjusted so that the computed eye position matched targets that were a known distance from the central fixation point.

Likewise, marmosets performed the VPLT while head-restrained and seated in a primate chair. All behavior was collected in a chamber illuminated only by a 21-in. LED display (X2411z, BenQ), which had a dynamic range from 0.5 to 230 cd/m^2, with luminance linearity verified by photometer. Background illuminance was 115 cd/m^2. Eye calibration was performed by fixating detailed marmoset faces (1°) and then finely adjusted with a central fixation spot (0.3°) at the center of the visual display. The VPLT was identical except that fixation lasted only 0.2–0.4 sec, the images subtended 10° of visual arc, and the interleaved calibration trials consisted of an array of up to eight marmoset faces, with reward delivered for maintaining fixation on a face for over half a second. Eye position was acquired at 220 Hz using an Eye Tracker and Viewpoint software (Arrington Research), with eye position collected from infrared light reflected off of a dichroic mirror (Part 64-472, Edmunds Optics). Eye calibration and the VPLT were controlled using a custom MATLAB GUI on a Windows 7 machine with Intel i7 CPU, 8 GB RAM, and GeForce Ti graphics card, which was presented on a second display. The software subsampled eye position online at the display refresh rate of 120 Hz using the ViewPoint MATLAB toolbox (Arrington) and presented visual stimuli using the PsychoPhysics Toolbox (Brainard, 1997; Pelli, 1997). Frame timing was confirmed by monitoring a photodiode (SD200-12-22-041-ND, Digi-Key).

Both species were head-restrained and oriented to the center of the visual display for all behavioral tasks. Both marmosets and macaques typically completed 400 VPLT trials (200 images, each shown twice) with the exception of Marmoset L, who completed behavioral sessions of 200 VPLT trials (100 images). This was done because Marmoset L inspected images for a longer time than any other subject, and we wanted to ensure as many complete behavioral sessions as possible.

Image Categorization

Images were sorted into three categories—objects, landscapes, and faces—by one of the authors (S. U. N.) and laboratory technician (M. G.) using the following instructions: Images with a distinct, nonbiological object or objects in the foreground were to be marked as "objects," images with no distinct object or subject in the foreground were to be marked as "landscapes," and images with a human or animal face clearly visible were to be marked as "faces." Not all images fit into these categories, and only images that both sorters marked as clearly falling within each category were used for this analysis, resulting in 685 objects, 465 landscapes, and 516 faces. Author S. U. N. marked the spatial extent of each face using ellipses on images categorized to include faces for further analyses.

Saccade Identification

Saccades were identified using previously described methods (Hafed, Goffart, & Krauzlis, 2009), including 8°/sec velocity criterion and 550°/sec^2 acceleration criteria for 1500 of the 3000 images. All saccades were manually inspected to confirm or modify the eye signal flagged as a saccade. Peak velocities and amplitudes were calculated to confirm all data conformed to the expected shape of the main sequence. Analyses were restricted to saccades 1° or greater, because the video-based eye tracking was unable to reliably detect microsaccades. All analyses were also performed using all identifiable saccades, which resulted in a higher frequency of saccades for all subjects but resulted in the same, significant results across species.

Experimental Design and Statistical Analysis

Subjects were shown up to 200 images in a single VPLT behavioral session from a database of 3000 images, and all subjects completed at least 80% of this image database. Nonparametric sign tests compared looking times for VPLT trials that presented novel images (novel trials) compared with trials that presented the same image a short time later (repeat trials), within single behavioral sessions, or within subjects across all behavioral sessions; visual recognition produced shorter looking times for repeat trials. Brown–Forsythe tests compared the variance in VPLT looking times across subjects, with Holm–Sidak correction for multiple comparisons. This analysis was performed only on VPLT trials that did not reach the 5-sec limit. Including those trials yields nearly identical results, except that, for novel VPLT trials, one comparison, Marmoset L to Macaque T, does not reach significance (p = .91). More detailed comparisons of subject behavior were performed for VPLT images that clearly fit into one of three categories (described above). Two-way ANOVA tested whether changes in looking time depended on subject species, category of image content, or an interaction between these groups. Differences between ANOVA groups were identified using Tukey's tests, correcting for multiple comparisons. A nonparametric sign test was used to measure species differences in the proportion of looking time spent looking at faces in images categorized to include face content. Pearson's correlations identified a relationship between novel trial looking times and the degree of visual recognition indicated by behavior (novel looking time minus repeat looking time). Saccadic eye movements were identified for half of our data set (1500 images). Median intersaccade intervals were compared across subjects using nonparametric rank-sum tests, with Holm–Sidak correction for multiple comparisons.

RESULTS

We compared the behavior of three marmoset and three macaque subjects performing a simple VPLT. Briefly,

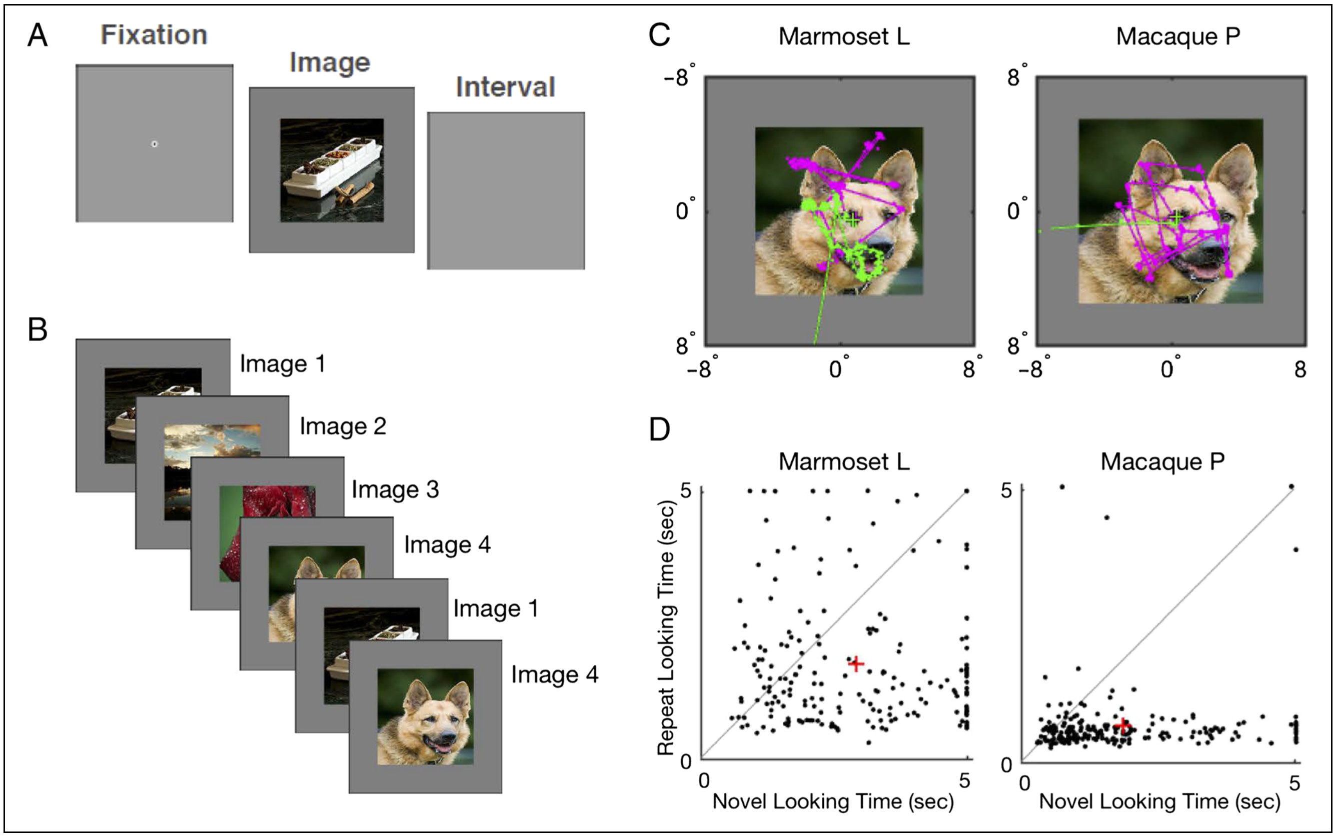


Figure 1. The VPLT and sample marmoset and macaque behavior. (A) Trials began with a period of central fixation followed by presentation of an image. The subject could freely view the image until it looked away or 5 sec had passed. A blank screen was displayed between consecutive trials. (B) An example schematic of a sequence of trials shows four novel trials, in each of which a novel image was shown to the subject. Following the novel trials, those images are shuffled and displayed again in the same number of repeat trials—the first two are shown in this panel. Blocks could consist of 6, 8, or 10 trials, in which three, four, or five images are presented exactly twice. (C) Sample looking behavior for one image from a marmoset (left) and a macaque subject (right). The eye position during the novel trial is indicated by the magenta traces and for the repeat trial by the green traces. (D) Viewing times for a sample session of 200 unique images from a marmoset subject (left) and a macaque subject (right) with the time spent looking at each image indicated by a black dot. Mean viewing times for all novel presentations compared with repeats are indicated by red crosses.

each VPLT trial presents an image (Figure 1A), and the trial ends when the subject first looks away from the image or after 5 sec has elapsed. The VPLT is organized in blocks of 6, 8, or 10 trials; the first half of the block consists of trials that display a completely novel image (novel trials). The rest of trials in the block display the same images from the novel trials, but in a randomized order (repeat trials). Figure 1B shows an example progression of an eight-trial block that started with four novel trials, followed by two repeat trials—the block would conclude after the remaining two images are repeated. Figure 1C shows example looking behavior from one marmoset and one macaque subject viewing an image. In this example, looking behavior during a novel trial is illustrated by the magenta eye traces and looking behavior for the repeat trial is illustrated by the green eye traces. In the novel trial, both subjects remained on the image for the entire 5 sec. However, on the repeat trial, both subjects looked away from the image before 5 sec elapsed, ending the trial. Figure 1D summarizes both macaque and marmoset performance for 200 images in the behavioral sessions that included the trials illustrated in Figure 1C. In both cases, marmosets and macaques tended to look at novel images for a longer time compared with the same image repeated a short time later (sign tests: marmoset, sign = 147, 200 images, $p < .0001$; macaque, sign = 176, 200 images, $p < .0001$). However, the marmoset subject tended to look at images for greater periods of time than the macaque. Moreover, the marmoset exhibits more variability in looking times compared with the macaque subject. The trend observed in the sample behavioral sessions are representative of data for all subjects over many behavioral sessions. Figure 2 summarizes VPLT performance of marmoset (A) and macaque (B) subjects over all sessions. All subjects showed strong looking preferences for novel images compared with repeated images (sign tests: Marmoset A, sign = 2271, 2735 images, $p < .0001$; Marmoset K, sign = 1753, 2814 images, $p < .0001$; Marmoset L, sign = 1996, 2990 images, $p < .0001$; Macaque I, sign = 1567, 2027 images, $p < .0001$; Macaque P, sign = 2054, 2400 images, $p < .0001$; Macaque T, sign = 2251, 2731 images, $p < .0001$; Figure 2A and B, top). This trend was observable in every

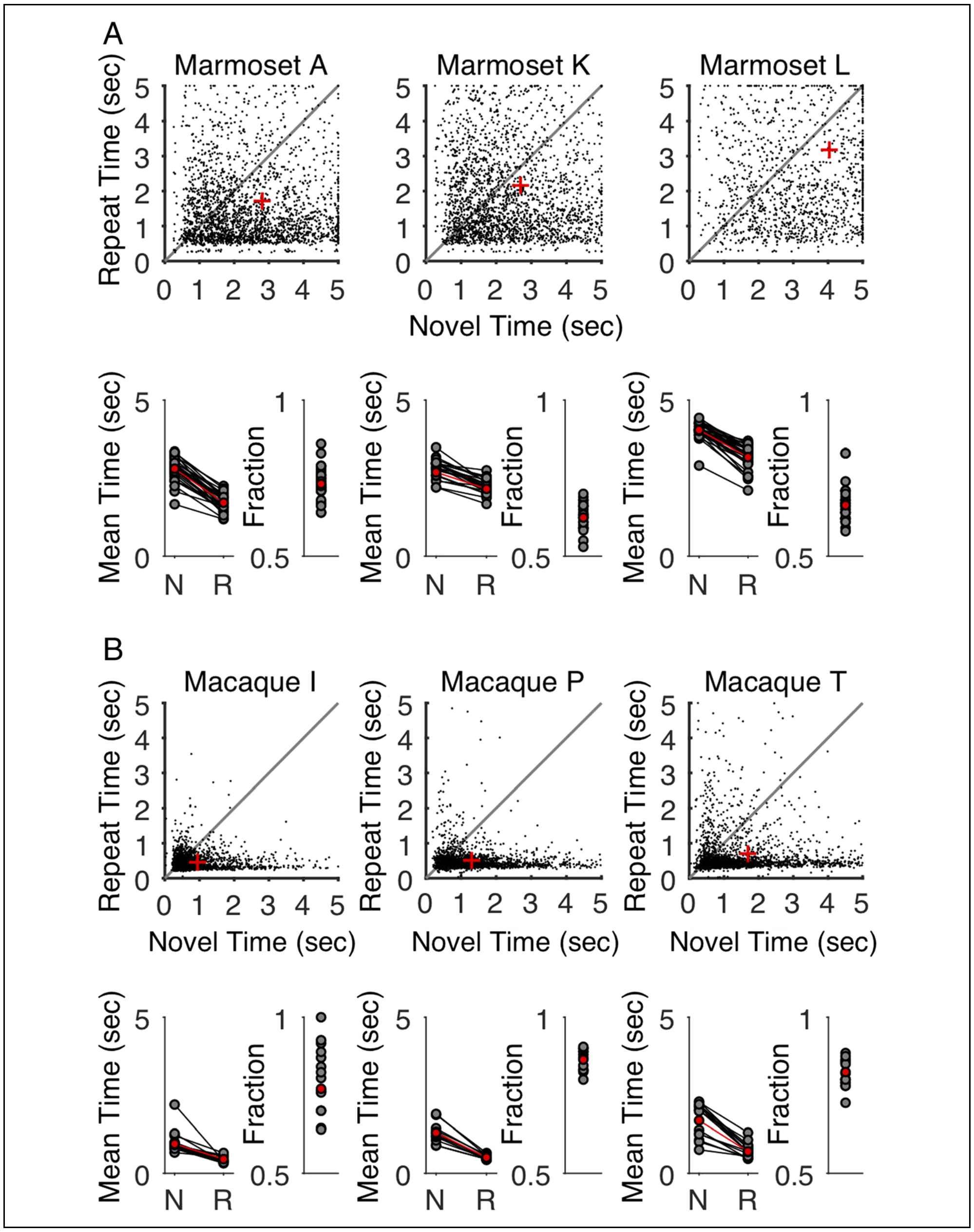


Figure 2. Marmosets and macaques look at novel images longer than recently viewed images. (A) Above, looking times for every image are plotted by black points for three marmoset subjects. Points below the unity line are images with longer looking times for the novel presentation compared with the repeat presentation. The red cross indicates the average looking time for novel compared with repeat presentations. Below, looking times are summarized for each behavioral session by plotting the mean looking time for novel image presentations compared with repeat presentations, with the summary for all images plotted in red. Results of individual sessions are also summarized by plotting the fraction images with greater novel presentation looking times, with the results over all images plotted in red. In both cases, marmosets show a preference for looking at novel stimuli in every behavioral session. (B) Looking preferences for three macaque subjects summarized using the same conventions as A.

individual behavioral session (Figure 2A and B, bottom), but marmoset subjects had longer looking times for both novel and repeat image presentations as well as greater trial-to-trial variability. Importantly, both marmoset and macaque monkeys demonstrate the same qualitative looking preference for novel images, with shorter looking times for the repeated presentation demonstrating occurrence of visual recognition for some subset of the images.

The greater variability for looking times in marmosets compared with macaques is more clearly observable in the distributions of looking times for each subject for both novel images (Figure 3A) and repeat images (Figure 3B). However, the shapes of looking time distributions in Figure 3 are difficult to quantify using a Gaussian standard deviation due to their asymmetric shape and the imposed 5-sec time limit for each image. To quantify this variability, we applied a Brown–Forsythe transformation to the standard deviation of looking time for each subject, which is more robust to non-Gaussian distributions. This estimate of variance was calculated after removing trials that reached the maximum 5 sec looking time to reduce the impact of that imposed ceiling on the looking time distributions. Notably, marmosets exhibited significantly greater variance in image looking times than macaques for all nine possible subject comparisons between species (i.e., Marmoset A to Macaques I, P, and T; Marmoset K to Macaques I, P, and T; Marmoset L to Macaques I, P, and T) for repeat VPLT trials and for novel VPLT trials (Brown–Forsythe tests, $p < .0001$).

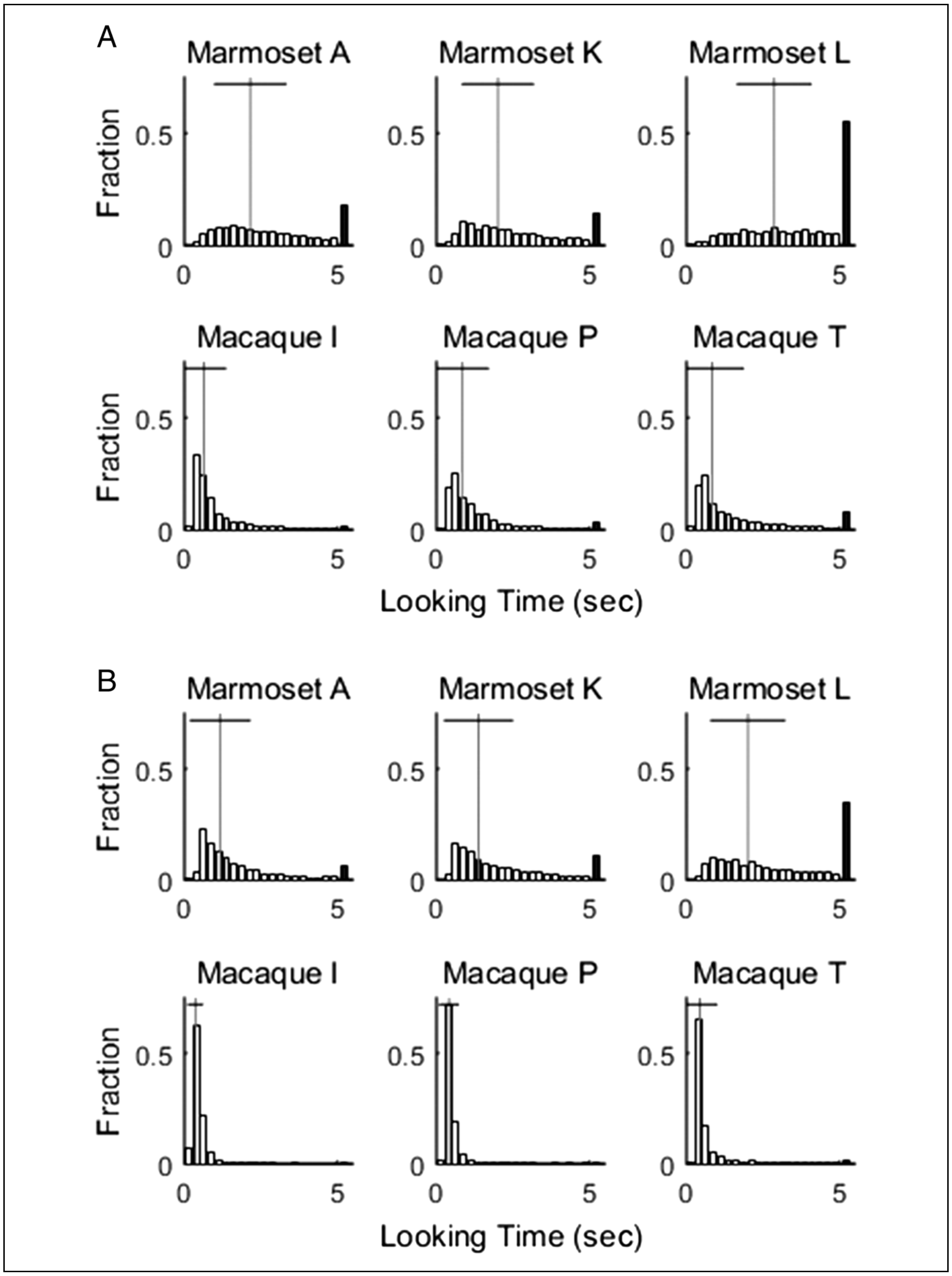


Figure 3. Marmoset looking time varies more than macaque looking time. (A) Comparison of distributions of looking times for marmosets (top) and macaques (bottom) for novel images. Histograms of looking times for each image are given, with looking times of 5 sec (maximum time images were displayed) plotted as a black bar. Median is provided by vertical gray lines, and the horizontal error bar at the top of median provides the Brown–Forsythe standard deviation for each subject of all trials, excluding those with the maximum looking time. (B) Comparison of distributions of looking times for marmosets and macaques for repeat images. Conventions are the same as A.

To search for deeper similarities in marmoset and macaque visual behaviors, we tested whether image content influenced this task by separately analyzing images that cleanly fit into categories of objects, landscapes, and faces (see Methods). Figure 4A shows looking times of every subject for each image category. Two-way ANOVA found looking time significantly depended on species and categories, but not on the interaction: species, $F(1, 6684) = 2180$, $p < .0001$; image category, $F(2, 6684) = 236$, $p < .0001$; interaction, $F(2, 6684) = 2.10$, $p = .12$. This resulted in two easily observable main effects. First, as previously observed, marmosets looked at images for longer periods of time than macaques. Second, faces resulted in the longest looking times for both species, followed by objects, with the shortest looking times reserved for landscapes with no distinct object or subject in the foreground (Tukey's test, $p < .0001$, for all comparisons). We found the novel looking time was strongly correlated with the looking preference (marmoset, $r(2787) = 0.65$, $p < .0001$; macaque, $r(3898) = 0.90$, $p < .0001$), resulting in the same pattern of results for looking preference as for novel looking time in Figure 4B. Two-way ANOVA found looking preference only depended on image content and not species (species, $F(1, 6684) = 0.25$, $p = .62$; image category, $F(2, 6684) = 28.2$, $p < .0001$; Tukey's test: objects and

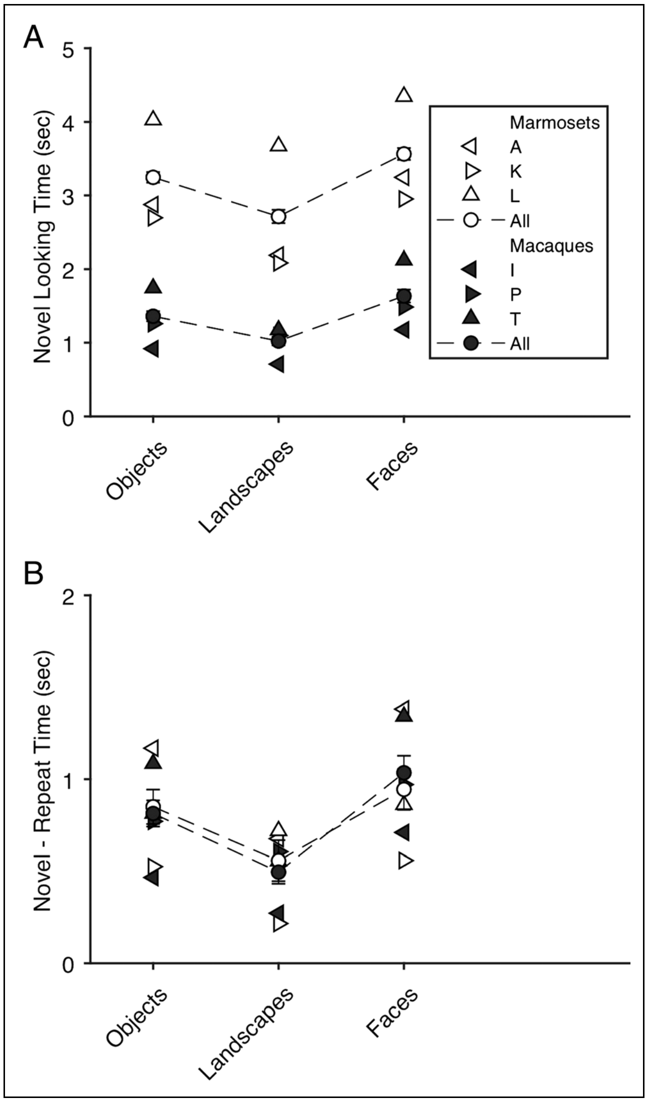


Figure 4. Novel image exploration and preference depends on image content. (A) Mean viewing times of novel images for each subject, separated by whether the image contained objects, faces, or was a landscape with no distinct item in the foreground. Error bars for the species-wise averages are 95% confidence intervals. (B) Mean novel preference (calculated by subtracting repeat looking times from novel looking times) for each subject, separated by image content. Error bars for the species-wise averages are 95% confidence intervals.

landscapes, $p < .0001$; objects and faces, $p = .010$; landscapes and faces, $p < .0001$).

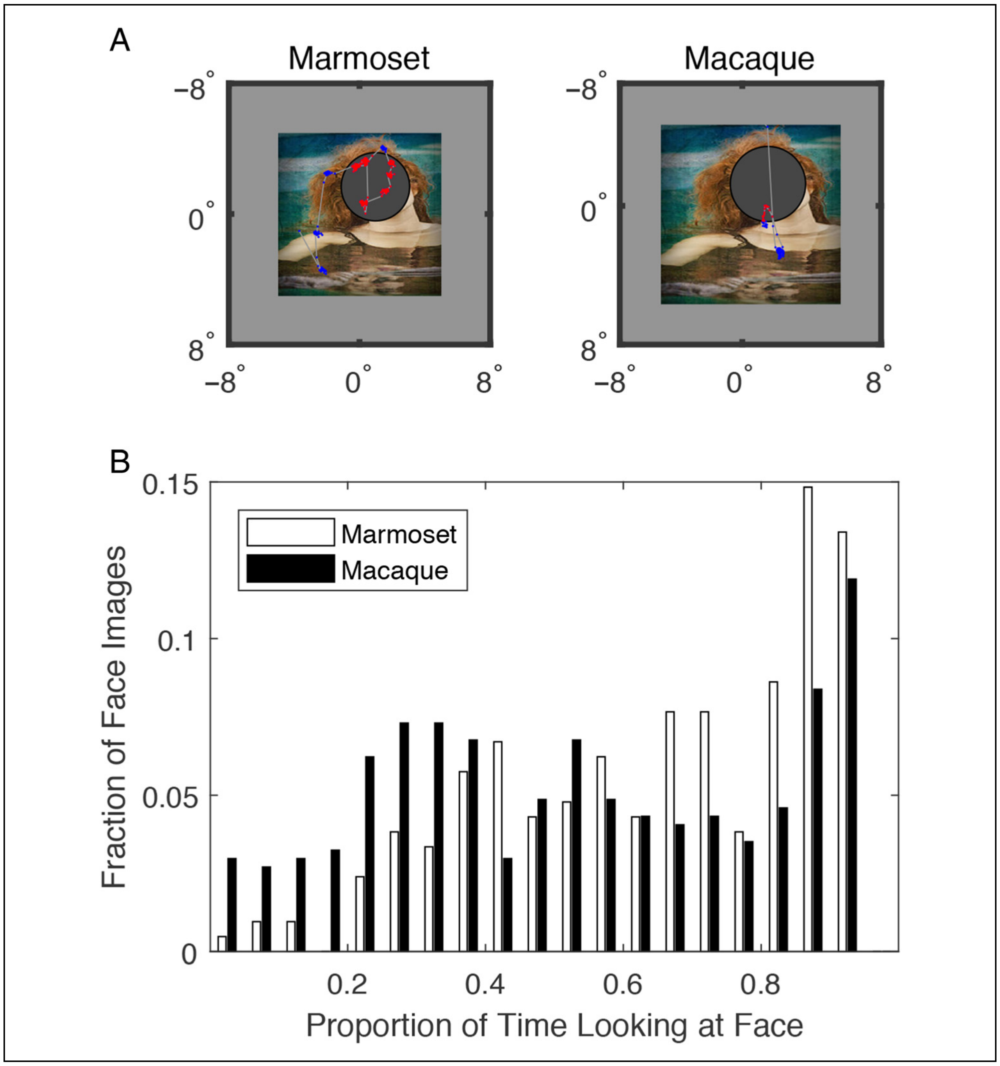
Because both species showed the greatest looking times and strongest looking preferences for faces, we performed an analysis to determine whether both species spent comparable amount of time looking at faces in these images compared with other parts of the image (Figure 5A). Figure 5B summarizes the distributions of time spent directly viewing the face parts of each image for marmosets (white bars) and macaques (black bars). This analysis was only performed for the initial, novel, image presentations. Whereas both species typically viewed face parts of images for a relatively large proportion of the total looking time (marmosets 79% median, macaques 73% median), marmosets had a significantly stronger proclivity to do so (sign test, sign = 117, 507 images, $p < .01$).

Because the largest observed differences between marmoset and macaque behavior were apparent in their looking behavior with regard to novel images, we examined the subjects' saccadic eye movements to look for other differences in active vision. In particular, we focused on saccades that reoriented gaze by more than 1° of visual arc. Figure 6 compares the distributions of intersaccade intervals for marmoset and macaque subjects. Strikingly, all marmosets showed significantly shorter intervals between such saccades, with medians of 259 msec for Marmoset A, 267 msec for Marmoset K, and 292 msec for Marmoset L and medians of 342 msec for Macaque I and 408 msec for Macaques P and T. All marmosets had significantly shorter intersaccade intervals than all macaque subjects (rank sum tests, $p < .0001$ after correction for multiple comparisons).

DISCUSSION

Here, we directly compared marmoset and rhesus macaque monkey behavior on a VPLT to precisely identify similarities and differences in visual recognition memory of these primate species. Importantly, we found the same qualitative pattern of recognition memory exhibited by rhesus macaques (Jutras & Buffalo, 2010; Wilson & Goldman-Rakic, 1984) and humans (Crutcher et al., 2009)—the preference for looking at novel images compared with familiar images (i.e., the second presentation). Although not a complete primate phylogeny, the evidence that species from at least three primate families—apes, New World monkeys, and Old World monkeys—exhibit notably similar patterns of recognition memory on this task is at least suggestive that the underlying processes may be conserved across all primates. To more fully test this hypothesis, however, additional species in these families, as well as prosimians, must be studied on the same task. In our comparison of rhesus macaques and marmosets, the greatest reduction in looking times occurred for faces followed by objects and then landscapes—the same order of looking times for image content when comparing across only novel image presentations. The interest in faces is consistent with its significant role in social signaling across primates (Taubert, Wardle, Flessert, Leopold, & Ungerleider, 2017; Freiwald, Duchaine, & Yovel, 2016; Hung et al., 2015a; Mosher, Zimmerman, & Gothard, 2014; Tsao, Moeller, & Freiwald, 2008; Tsao, Freiwald, Tootell, & Livingstone, 2006; Kanwisher, McDermott, & Chun, 1997). Data presented here suggest that attention to faces across both species of nonhuman primates may increase the likelihood that features of this social object are recognized over other salient objects and facilitate broader face recognition processes (Landi & Freiwald,

Figure 5. Marmosets look directly at faces more often than macaques. (A) An example image demonstrates how the proportion of time spent looking directly at faces was calculated, with the eye trace from a marmoset (left) and a macaque (right) subject. Faces in each image were marked by ellipses, and the proportion of time the eye was directed into the face region (red points) was divided by the proportion of time the eye was directed out of the face region (blue points). (B) The distribution of the proportion of time looking directly at faces for marmosets (white bars) is shown compared with macaques (black bars). All subjects were pooled for clarity.



2017). Consistent with previous studies (Mitchell et al., 2014), these data suggest that marmosets and macaques exhibit broadly similar patterns of visual cognitive behavior. However, more detailed comparisons revealed significant differences across the species.

Further quantitative comparisons of recognition memory between marmosets and rhesus macaques were confounded by striking, unexpected differences in the active scanning of images that were independent of image familiarity. For ease of reader reference, these differences are summarized in Table 1. Most noticeably, marmosets exhibited longer looking times than rhesus macaques regardless of image content or familiarity. The increased looking times in marmosets were accompanied by an increase in the variability of looking times—apparent for both novel and familiar images—and complicates further direct comparisons of the degree of visual recognition between marmosets and rhesus macaques. We find that marmosets less consistently exhibited looking preference for novel images compared with macaques, but this could be due to either the greater variability in their looking behavior or to a lower frequency of recognition occurrence. These differences in visual behavior of marmosets and rhesus macaques limit further discussion of our results with regard to recognition memory, but they point to interesting differences in visual processing between the species.

Primate vision includes many facets of feature processing, selection, and control over eye movement. Visual processing in precortical and cortical areas seems unlikely to cause the large behavioral differences we observed between rhesus macaques and marmosets, because both subjects share preferences for image content, including a strong preference for faces. In fact, deeper analysis demonstrated marmosets to have an even greater tendency to look at faces than macaques. The observed differences are better explained by differences in the active control of eye movements; specifically, we suggest that rhesus macaques and humans are more easily able to inhibit eye movement to distractors. Strong inhibition is necessary for macaque gaze aversion to suppress overt attention to salient facial features that also can signal aggression (Chance, 1967). In addition, it is fast and routine to condition rhesus macaques to

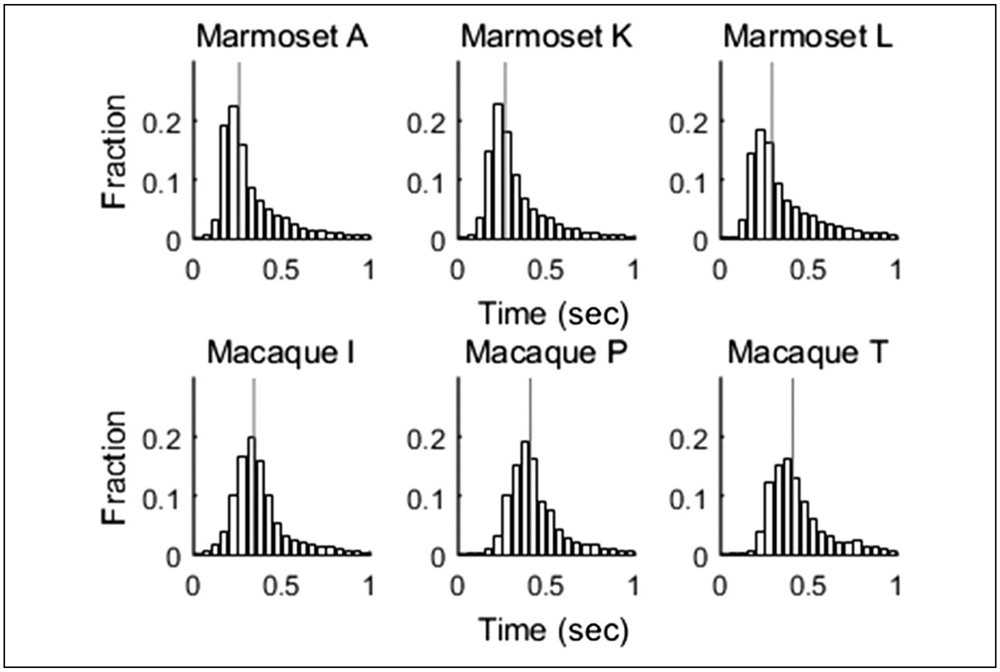


Figure 6. Saccade frequency is greater for marmosets compared with macaques. Distributions of intervals between saccades greater than 1° in amplitude for the same set of 1500 novel images are provided for each marmoset (top) and macaque (bottom) subjects. Vertical gray lines indicate the median intersaccade interval.

maintain fixation, even in the presence of many salient distractors (Mitchell, Sundberg, & Mitchell, 2009; Allman, Miezin, & McGuinness, 1985), yet it is difficult to train marmosets to maintain fixation, or smooth pursuit, for many seconds, even without salient distractors (Mitchell, Priebe, & Miller, 2015; Mitchell et al., 2014). We found that marmosets exhibited more frequent saccadic eye movements greater than 1° in amplitude, with median intersaccade intervals of about 256 msec in marmoset compared with 375 msec in rhesus macaques. One specific mechanism that could cause such differences is a reduced suppression of alternative saccade plans in the FEF (Schall, Hanes, Thompson, & King, 1995) or superior colliculus (Krauzlis, Liston, & Carello, 2004), possibly due to weaker recurrent or lateral inhibition from the neurons active during fixation (Munoz & Wurtz, 1993a,

Table 1. Summary of Subject Behavior on the VPLT

	Median Looking Time (sec)			*SD (Brown–Forsythe)*		*Median ISI (sec)*	
	Novel	*Repeat*	*Difference*	*Novel*	*Repeat*	*Novel*	*Trials per Session*
Marmoset							
A	2.59	1.23	0.99	1.19	1.01	259	400
K	2.37	1.63	0.48	1.18	1.14	267	400
L	5	3.18	0.53	1.23	1.24	292	200
Mean	3.32	2.01	0.67	1.2	1.13	272	
Macaque							
I	0.63	0.36	0.24	0.74	0.26	342	400
P	0.87	0.41	0.41	0.87	0.33	408	400
T	0.94	0.44	0.38	1.04	0.58	408	400
Mean	0.81	0.4	0.34	0.88	0.39	386	
Species diff	2.51	1.61		0.32	0.74	−114	

The table provides a quick reference of several important metrics of macaque and marmoset behavior on the VPLT. The first three columns report the median amount of time subjects spent looking at novel image presentations, repeat image presentations, and the difference between novel and repeat looking times, respectively. Columns 4 and 5 report the Brown–Forsythe standard deviations of looking time for novel and repeat image presentations. Column 6 reports the median intersaccadic intervals (ISIs) during image presentations for novel images. Column 7 reports the number of image presentations, or trials, in a behavioral session.

1993b). Other possibilities include differences in connectivity between gaze control areas, for example, one report indicated sparse or absent projections from supplementary eye fields to the superior colliculus in the marmoset (Collins, Lyon, & Kaas, 2005). Direct evidence for these hypotheses could be collected by applying standard electrophysiological techniques used in macaques to the marmoset FEF and superior colliculus during a simple stimulus discrimination task. Other possible explanations include differences in the circuitry underlying covert visual attention or visual selection, which is strongly associated with memory (Broadway, Hilimire, & Corballis, 2012; Ballesteros, Reales, García, & Carrasco, 2006). However, these mechanisms may be intertwined, as suppression of distractors may enhance recognition memory (Markant, Worden, & Amso, 2015) and some attributes of visual attention depend on gaze control structures (Zénon & Krauzlis, 2012; Moore & Fallah, 2004).

Here, we found broad similarities in marmoset and rhesus macaque behavior, indicating the formation of recognition memories, with more reliable indications of memory for faces compared with objects or landscapes. However, we also observed substantive differences in their active vision that merits further investigation at the neurobiological level. Direct comparisons of behavior between primate species enable us to form key predictions about the nuanced relationship between differences in behavior and cognition across the Order and the supporting neural processes. The almost exclusive reliance on rhesus macaques for the past 30 years of research has significantly limited our capacity to leverage the power of phylogenetic analysis to explicate these issues. Comparatively studying marmosets and other closely related species in the taxa affords the unique opportunity to better understand many mechanisms most relatable to humans, such as those supporting social interaction, visual navigation, object recognition, decision-making, and memory.

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