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Visual Processing Speed in Capuchin Monkeys (*Cebus apella*) and Rhesus Macaques (*Macaca mulatta*)

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Visual acuity is a defining feature of the primates. Humans can process visual stimuli at extremely rapid presentation durations, as short as 14 ms. Evidence suggests that other primates, including chimpanzees and rhesus macaques, can process visual information at similarly rapid rates. What is lacking is information on the abilities of New World monkeys, which is necessary to determine whether rapid processing is present across the primates or is specific to Old World primates. We tested capuchin (*Cebus apella*) and rhesus (*Macaca mulatta*) monkeys on a computerized matching-to-sample paradigm to determine the shortest presentation duration at which stimuli could be correctly identified. In Study 1, using clip art images, both species achieved presentation durations as short as 25 ms while maintaining high accuracy rates. In Study 2, we used logographic Asian language characters to see if stimuli that were more similar in appearance would reveal species differences. Neither species was as accurate, or achieved as short of presentation durations, as with clip-art images. In particular, capuchins were initially less accurate than rhesus in Study 2, but with experience, achieved similar accuracy rates and presentation durations. These data indicate that rapid visual processing abilities are widespread in the primate lineage, and that the form of the stimuli presented can have an effect on processing across species.

A hallmark of the primates is a reliance on vision, including rapid processing of visual information. The fitness benefits of being able to do so likely include everything from predator detection to finding food. Humans are the primates that have been the most studied with regards to visual processing, and they can process and consciously recall visual stimuli presented at durations as short as ~200 ms (Bartz, 1962). Additionally, humans can process visual information without conscious awareness, responding accurately to visual stimuli that they do not consciously recall having seen that were presented for durations ranging from 50 ms (Bar & Biederman, 1998; Debner & Jacoby, 1994) to as little as 14 ms (Keysers, Xiao, Földiák, & Perrett, 2001).

Other primates can process visual stimuli as rapidly as humans in some contexts. Chimpanzees (*Pan troglodytes*), one of the two closest living relative to humans, can process and sequence number arrays after having seen the array for only 210 ms (Inoue & Matsuzawa, 2007). Although these chimpanzees outperform inexperienced humans, humans trained on this same task can still outperform chimpanzees (Cook & Wilson, 2010). Considering Old World monkeys, data from single-cell recordings indicate that the neurons of rhesus macaques (*Macaca mulatta*) are able to discriminate between stimuli presented for 14 ms, the minimum seen in subconscious visual perception in humans (Keysers et al., 2001). Keysers and colleagues also tested humans on a similar paradigm, albeit without single-cell recording. As with the monkeys, humans were able to respond at above chance levels even at 14 ms presentation durations, providing behavioral evidence to complement that from the monkeys' neuronal responses. New World monkeys, on the other hand, have not been tested with as rapid presentation durations as macaques and humans. Capuchin monkeys (*Cebus apella*) show high accuracy in delayed memory tasks with

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presentation durations of 75 ms (D'Amato & Worsham, 1972; Worsham, 1975), but have not been assessed at faster durations.

What is lacking, then, are data comparing the visual processing speeds of New World monkeys to that of the other primates when there is not a memory component of the task (e.g., a forced delay before response) and at very short (e.g., < 50 ms) durations. Examining a species that is more distantly related to apes and Old World monkeys can provide indication of whether rapid processing speed is a trait present throughout the primate lineage, as we suspect, or one that emerged more recently, after New World monkeys diverged from the rest of the primates around 42 mya (Steiper & Young, 2006), due to more specialized needs. Of course, while a study exploring only two species cannot rule out convergence due to similar selective pressures unique to the species under consideration, the reasons that rapid visual processing abilities are anticipated in the primates are widespread across the taxon, making it less likely that this is the case.

We investigated visual processing speed in the capuchin monkey (*Cebus apella*), a New World monkey which converges with humans and chimpanzees on several traits that might indicate the need for fast processing times, which, as discussed above, helps to rule these out as potential confounds to a phylogenetic analysis (although note that all of the primates are reliant on vision, indicating that selective pressures for visual processing speed and acuity are likely multi-factorial). In particular, capuchins have large brains compared to their body size, on par with that of chimpanzees (and larger than that of rhesus, although rhesus have a larger absolute brain size; (Rilling & Insel, 1999), and live in large social groups (Fragaszy, Visalberghi, & Fedigan, 2004), as do both humans and rhesus. In addition, the behavior and ecology of capuchin monkeys suggests a need for rapid processing of visual information. Like chimpanzees, but unlike many primates, including rhesus, they gain a large percentage of their diet from the capture of live vertebrate and invertebrate prey, which can move quickly as well as blend into the environment. Additionally, unlike either rhesus or chimpanzees, these small-bodied, arboreal monkeys reside in the tropical forests of Central and South America, where they are targets for avian and terrestrial predators (Fragaszy et al., 2004). These traits suggest that capuchins may have been selected to process visual information rapidly, either for similar reasons as were the apes and Old World monkeys or due to other ecological pressures. Thus for both phylogenetic and ecological reasons, it is reasonable to anticipate that capuchin monkeys should have visual processing speeds on par with those of the other Old World monkeys and apes that have been tested thus far.

Our goal was to identify the shortest presentation duration for a single image at which capuchin monkeys could correctly identify the stimuli, and then, using the same stimuli, to compare this to the shortest presentation duration achieved for rhesus macaques, an Old World monkey, who diverged from the ape lineage around 31 mya (Steiper & Young, 2006). Rhesus macaques are a useful species for such a comparison, as there are already data indicating that they can process visual stimuli rapidly (Keyes et al., 2001). Using these two species will provide the comparison of New and Old World monkey visual processing that is lacking in the literature and essential to begin to understand the distribution of visual processing speeds across this visually reliant taxon. We measured visual processing behaviorally, identifying whether members of these two monkey species could correctly identify the match in a computerized matching-to-sample task with a systematically decreasing presentation time for the sample. We predicted, based on the ecology of capuchin monkeys as well as the general reliance on vision evidenced in all non-human primates, that they would be able to respond as accurately as rhesus macaques on this task.

Study 1

Method

We tested eight capuchin monkeys (male = 4, female = 4; age range = 3-18 years old; mean age = 9 years old) and six rhesus macaques (male = 6; age range = 8 – 28 years old; mean age = 16.6 years old) from the Language Research Center of Georgia State University, Atlanta, Georgia. All monkeys had *ad libitum* access to water and were fed chow, fresh fruits and vegetables, and enrichment items several times throughout the day. Animals were never food or water deprived for the purposes of testing. The Institutional Animal Care and Use Committee of Georgia State University approved all testing procedures. Software for this experiment was written in Visual Basic, version 6.0. Trials were presented on a 17-inch color monitor attached to a personal computer, with an interface to a pellet dispenser that automatically rewarded correct responses.

Capuchins and rhesus macaques are both proficient at processing pictures (e.g., *Cebus*: Truppa, Spinozzi, Stegagno, & Fagot, 2009; *Macaca*: Orban, 2008). Additionally, our subjects had previously been trained to use a joystick to complete computerized cognitive tasks. For details of that training, see Evans, Beran, Chan, Klein, and Menzel (2008) for capuchin monkeys and Rumbaugh, Richardson, Washburn, Savage-Rumbaugh, and Hopkins (1989) for rhesus macaques. Monkeys controlled a cursor on the computer screen by using a joystick, and moved the cursor into contact with visual stimuli on the screen to select an image. We chose a matching-to-sample (MTS) program because it is an ideal paradigm to determine whether subjects are able to report which of two images was seen previously. Additionally, all monkeys had prior experience with this paradigm, thus there was little risk that their visual processing speed would be confounded with the challenges of learning a novel task.

Stimuli consisted of black and white clip art images. To start each trial the monkeys had to move the cursor into contact with an orienting icon (a grey square) to assure they were paying attention. Immediately after selecting the orienting icon, subjects were shown the sample stimulus for a predetermined duration (see below). Then, the sample was immediately covered with a black rectangle so as to prevent any visual afterimage from occurring. Two match choices appeared onscreen simultaneously with the black rectangle. The match images appeared in two of six randomly chosen locations around the perimeter of the screen. Monkeys had to choose between an image that was an identical match to the sample and a foil stimulus (See Figure 1). A correct response led to a single sweetened pellet that was automatically dispensed by the computer (i.e., no humans were present during testing, eliminating the possibility of cuing the animals). After a correct response there was a 1-s inter-trial interval. An incorrect response led to a 3-s timeout period during which the screen remained blank (and no pellet was given).

The program was designed to titrate the sample stimulus presentation duration to reach the shortest duration at which the subject could correctly identify the sample. Thus, whenever a monkey scored 16 out of 20 trials correctly in a 20-trial block, the presentation speed was reduced by 25 ms for the subsequent trial blocks. All animals started at a presentation speed of 150 ms in each session. Durations could ultimately be reduced to 25 ms, which was the fastest reliable presentation speed given our hardware and software. The presentation duration never increased during a session, regardless of the subject's performance. Each animal worked or rested as they chose over the course of a session, and they completed as many sessions as necessary to complete 1,000 trials. Thus, the number of test sessions varied across animals (capuchin mean = 2.4 sessions; range = 2-3 sessions; rhesus mean = 1 session; range = 1 session). No animal ever completed fewer than 200 trials in one session. Thus, there were a sufficient number of trials for each animal to reach the shortest presentation duration within each session. The stimulus presentation duration returned to 150 ms at the start of each new session.

We analyzed both the first 200 trials and the last 200 trials for each animal. We chose to do the analysis in this way for two reasons. First, we wanted to see how animals performed with a brief exposure to this task so that experience would not affect their results (i.e., the first 200 trials). This also helped us address the issue of animals taking different numbers of sessions to complete the task, as each animal completed at least 200 trials in the first session. Second, we used the last 200 trials to investigate the lowest presentation durations the animals could achieve at their most mature performance levels in this experiment. Examining only the last 200 trials allowed us to do so without confounds if some animals took longer than others, as well as avoiding the species differences in the number of sessions required to complete 1000 trials. Note that it was difficult for us to explore learning quantitatively due to the different number of sessions required to reach 1000 trials, however we can comment qualitatively on differences in accuracy between the first 200 and last 200 trials.

Given our small sample sizes, all statistics were non-parametric. We used binomial tests to compare accuracy levels to chance and Mann-Whitney tests to compare species' performance levels.

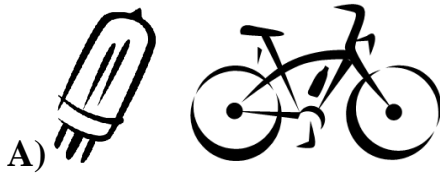


Figure 1. Example stimuli. **A)** Study 1 - clip art; **B)** Study 2 – logographic Asian language characters

Results & Discussion

In the first 200 trials, all animals correctly selected the match over the foil stimulus at levels significantly better than chance (binomial test: $p < 0.05$; See Table 1 for data on each individual), indicating they successfully discriminated the stimuli at whatever presentation duration they achieved in those first 200 trials. There were no significant differences between the species in either the accuracy rates (Rhesus: mean accuracy = 72.4%, range = 65.5-78.5%, SE = 1.9; Capuchins: mean accuracy = 68.1%, range = 58-88.5%, SE = 3.4; Mann Whitney U = 12.5, $p = 0.137$) or the shortest presentation duration achieved (Rhesus: mean duration = 120.8 ms, range = 25-150 ms, SE = 9.4; Capuchins: mean duration 125.3 ms, range = 25-150 ms, SE = 10.2; Mann-Whitney U = 19.5, $p = 0.560$).

The last 200 trials always occurred during the last test session, if there was more than one session required. All animals correctly selected the match over the foil stimulus at levels significantly better than chance (binomial test; $p < 0.05$), indicating that they were successfully discriminating the stimuli at whatever presentation duration they had attained by trials 800-1000. See Table 1 for data on individual monkeys.

With respect to the presentation duration, all macaques were at the shortest possible presentation duration, 25 ms, across the last 200 trials. The capuchins' average duration of presented stimuli during these trials was 46 ms (range: 25 ms – 150 ms; SD: 29.7). Three capuchins (Nala, Liam and Gabe) averaged 25 ms over their last 200 trials (see Table 1 for data on individual monkeys). Two capuchins (Wren and Logan) reached 25 ms, but not until they were already in the last 200 trials, so they averaged a longer duration. An additional three capuchins never reached the 25 ms duration.

Table 1
Individual performance in study 1

Species	Individual	Shortest Duration Achieved in ms		Average Presentation Duration in ms		Percent Correct			
		First 200 Trials	Last 200 Trials	First 200 Trials	Last 200 Trials	First 200 Trials	Last 200 Trials	First 200 Trials	Last 200 Trials
Capuchin	Drella	125.0	75.0	145.0	89.4	58.0	*	63.5	**
	Gabe	25.0	25.0	62.5	25.0	88.5	*	94.0	**
	Griffin	150.0	75.0	150.0	91.6	63.5	**	61.5	**
	Liam	100.0	25.0	132.5	25.0	67.0	**	66.0	**
	Lily	100.0	50.0	127.5	58.1	63.5	**	67.5	**
	Logan	150.0	25.0	150.0	25.4	60.5	*	69.5	**
	Nala	100.0	25.0	125.0	25.0	70.5	**	77.5	**
	Wren	75.0	25.0	110.0	28.8	73.5	*	70.0	**
	Average	103.1	40.6	125.3	46.0	68.1	**	71.2	**
Rhesus	Chewie	75.0	25.0	112.5	25.0	70.5	**	67.0	**
	Hank	125.0	25.0	147.5	25.0	72.0	**	70.5	**
	Lou	125.0	25.0	140.0	25.0	65.5	**	66.0	**
	Luke	100.0	25.0	132.5	25.0	71.5	**	64.0	**
	Murph	50.0	25.0	105.0	25.0	76.5	**	71.5	**
	Obi	25.0	25.0	87.5	25.0	78.5	**	68.5	**
		Average	83.3	25.0	120.8	25.0	72.4	**	67.9

* Denotes a score that is significantly above chance (binomial test; $p < 0.05$)

** Denotes a score that is significantly above chance (binomial test; $p \leq 0.001$)

When comparing the species, there was not a difference between accuracy (Rhesus: mean accuracy = 67.9%, range = 64-71.5%, SE = 1.2; Capuchins: mean accuracy = 71.2%, range = 61.5-94%, SE = 3.7; Mann-Whitney; $U = 23.5$, $z = -0.065$, $p = 0.950$) or shortest presentation duration over the last 200 trials (Rhesus: all individuals achieved 25 ms across the last 200 trials; Capuchins: mean duration 46 ms, range = 25-100 ms, SE = 10.5; Mann-Whitney; $U = 9$, $z = -2.257$, $p = 0.059$), although there was a trend for the macaques to have reached a shorter presentation duration. However, this was likely due to the macaques completing all 1000 trials within the first session, while the capuchins each took multiple sessions. This was because in each session, the presentation durations started over at 150 ms. Thus, because the capuchins took more sessions to complete 1000 trials, they had restarted at 150 ms more recently than the macaques, potentially leading to elevated average presentation durations over the last 200 trials.

In this task, all rhesus macaques and five out of eight capuchin monkeys were able to discriminate the clip art images at durations as short as 25 ms, and there were no significant differences between the species. This suggests that both capuchin monkeys and rhesus macaques are equally able to rapidly process visual information at duration speeds as short as 25 ms, confirming our hypothesis. However, 11 of our 14 monkeys were able to reach the shortest presentation duration possible with our technology. This suggests that we may be seeing a ceiling

effect due to high processing fluency, rather than truly exploring the limits of the abilities of these species. It may be that while the two species perform equally well at 25 ms using stimuli that are relatively easier to discriminate, species differences would emerge at either shorter presentation durations or with stimuli that were relatively more difficult to discriminate. Due to the limits of our technology, we were unable to test durations shorter than 25 ms. However, our stimuli, clip art, varied on multiple dimensions. Thus, we could alter the similarity of the stimuli, making them more similar to one another (e.g., reducing the variability), effectively decreasing their processing fluency, to see if one species was better able to distinguish between these more similar images at these short presentation durations

Study 2

Method

All of the same animals from Study 1 were used in Study 2. Additionally, all aspects of the methodology were the same. However, we changed the type of stimuli that were presented. Instead of clip art images of objects that differed on multiple dimensions (e.g., a light bulb versus a bicycle, which differ on shape, structure, etc.) monkeys were presented with computer generated logographic Asian language characters (e.g., Kanji & Mandarin; see Figure 1) that they had never seen before. These Asian characters differed from each other less than did the different clip art images. A computerized algorithm (Awesome Duplicate Photo Finder v. 1.0.1) found no clip art stimuli that were similar, all receiving similarity scores of 0%. However, with the Asian characters 10 out of 49 images were similar enough to be marked as potentially duplicate images with similarity scores that varied from 6-22% (an exact copy of an image would score 100%). Again the monkeys were given as many sessions as it took them to reach 1,000 trials (capuchin mean = 2.9 sessions; range = 2-4 sessions; rhesus mean = 1.2 sessions; range 1-2 sessions), and again all subjects completed at least 200 trials in every trial. Again, we chose to analyze the first and last 200 trials to see how monkeys performed with little exposure and with more experience on the task. We predicted that the monkeys would be less able to process these more similar stimuli at similarly rapid presentation durations as compared to the previous study that used the more distinctive clip art stimuli. We also predicted that species differences would be more likely to emerge in this more challenging context, although we had no directional prediction.

Results & Discussion

As in Study 1, accuracy was high for most animals in the first 200 trials. All animals except for three capuchin monkeys (Gabe, Griffin, and Lily) correctly selected the match over the foil stimulus at levels significantly better than chance (binomial test: $p < 0.05$; See Table 2 for data on each individual), indicating they successfully discriminated the stimuli at whatever presentation duration they achieved in the first 200 trials. In contrast to Study 1, rhesus monkeys were significantly more accurate than capuchin monkeys (Mann Whitney $U = 46.0$, $z = 2.8$, $p = 0.003$; Rhesus: mean accuracy = 64.8%, range = 61.5-68%, SE = 1.0; Capuchins: mean accuracy = 58.2%, range = 51-63%, SE = 1.3). However, there was no difference in the achieved presentation duration (Rhesus: mean duration = 140.4 ms, range = 75-150 ms, SE = 7.4; Capuchins: mean duration 147.2 ms, range = 125-150 ms, SE = 2.5; Mann-Whitney $U = 19.5$, $p = 0.560$). Therefore, in the first 200 trials with more similar images that, rhesus monkeys were no faster than capuchin monkeys, but were more accurate.

Table 2
Individual performance in study 2

Species	Individual	Shortest Duration Achieved in ms		Average Presentation Duration in ms		Percent Correct	
		First 200 Trials	Last 200 Trials	First 200 Trials	Last 200 Trials	First 200 Trials	Last 200 Trials
Capuchin	Drella	150.0	150.0	150.0	150.0	63.0 **	61.0 *
	Gabe	150.0	125.0	150.0	147.3	55.5	65.5 **
	Griffin	150.0	125.0	150.0	137.3	57.0	66.0 **
	Liam	150.0	50.0	150.0	50.0	60.0 *	58.5
	Lily	150.0	100.0	150.0	105.5	51.0	62.5 **
	Logan	125.0	75.0	130.0	98.5	60.5 *	67.0 **
	Nala	125.0	100.0	147.5	110.3	58.0 *	69.0 **
	Wren	150.0	100.0	150.0	100.0	60.5 *	61.0 *
	Average	143.8	103.1	147.2	112.3	58.2 *	63.8 **
Rhesus	Chewie	150.0	150.0	150.0	150.0	61.5 **	61.5 **
	Hank	125.0	25.0	137.5	57.5	66.5 **	70.0 **
	Lou	150.0	50.0	150.0	50.0	68.0 **	69.5 **
	Luke	150.0	50.0	150.0	72.5	62.5 **	66.5 **
	Murph	150.0	75.0	150.0	75.0	65.5 **	64.5 **
	Obi	75.0	25.0	105.0	25.0	65.0 **	57.0
	Average	133.3	62.5	140.4	71.7	64.8 **	64.8 **

* Denotes a score that is significantly above chance (binomial test; $p < 0.05$)

** Denotes a score that is significantly above chance (binomial test; $p \leq 0.001$)

In the last 200 trials, we found no differences between the primate species on either presentation duration (Capuchins: mean duration = 112.3 ms, range: 50 ms – 150 ms, SE = 11.6; Rhesus: mean duration = 71.67 ms, range: 25 ms – 150 ms, SE = 17.3; Mann-Whitney U = 11, $z = -1.682$, $p = 0.108$) or accuracy (Capuchins: mean accuracy = 63.8%, range: 58.5-69%, SE = 1.3; Rhesus: mean accuracy = 64.8%, range: 57–70%, SE = 2.0; Mann-Whitney U = 29.0, $z = -0.646$, $p = 0.573$), similar to what was found in Study 1. This suggests that while rhesus monkeys were initially more accurate with Asian characters than were capuchin monkeys, with experience capuchin monkeys were able to respond as accurately and discriminate images with as short of presentation durations as rhesus monkeys.

When comparing within species performance in the first 200 trials of Studies 1 and 2, capuchin monkeys performed similarly, with no difference between either presentation duration (Wilcoxon Signed-Rank Test: $z = -1.9$, $p = 0.063$) or accuracy (Wilcoxon Signed-Rank Test: $z = -1.8$, $p = 0.073$), although there was a trend toward shorter durations and higher accuracy in Study 1 as compared to Study 2. However, in the last 200 trials capuchins were both more accurate (Wilcoxon Signed-Rank Test: $z = -2.1$, $p = 0.036$) and achieved shorter presentation durations (Wilcoxon Signed-Rank Test: $z = -2.5$, $p = 0.012$) in Study 1 than in Study 2. Thus, while capuchin monkeys achieved high accuracy and rapid presentation durations in each study, they

were better able to discriminate between clip art images than Asian language characters in the last 200 trials (and showed a trend in this direction in the first 200 trials), despite the additional experience that they had received by having completed Study 1.

As with capuchin monkeys, rhesus monkeys achieved similar presentation durations over the first 200 trials of the two studies (Wilcoxon Signed-Rank Test: $z = -1.9$, $p = 0.058$), but again the trend was toward shorter presentation durations in Study 1. However, rhesus monkeys were significantly more accurate in the first 200 trials of Study 1 than Study 2 (Wilcoxon Signed-Rank Test: $z = -2.0$, $p = 0.046$), suggesting that they were better able to discriminate between clip art than Asian language characters with brief exposures to the stimulus sets, even at marginally faster presentation durations. In contrast to capuchin monkeys, rhesus monkeys were equally accurate on the last 200 trials of the studies (Wilcoxon Signed-Rank Test: $z = -1.153$, $p = 0.249$), although, like capuchin monkeys, rhesus monkeys achieved shorter presentation durations in the last 200 trials of Study 1 as compared to Study 2 (Wilcoxon Signed-Rank Test: $z = -2.0$, $p = 0.043$). Thus, rhesus were, like capuchins, better able to reach shorter presentation durations with clip art images than with Asian language characters.

General Discussion

Both capuchin monkeys and rhesus monkeys performed accurately at short presentation durations with stimuli that differed on both more and fewer dimensions. This provides evidence in favor of our prediction that, due either to phylogeny (e.g., primates' reliance on vision compared to the other senses) or ecological pressures (e.g., foraging techniques), capuchins would be similarly rapid and accurate as rhesus monkeys at short presentation durations. In Study 1, using clip art images, capuchin monkeys and rhesus monkeys were equally able to discriminate between the match and a foil stimulus at presentation durations (25 ms) that are at the lower end of the range of human perception without awareness (e.g., 14-50 ms). However, many individuals reached ceiling level performance with these simple stimuli. Therefore, we included a second study using stimuli that were harder to differentiate from each other to decrease processing fluency and see if any species differences were revealed. In the last 200 trials of Study 2, the monkeys of both species were unable to achieve as short of presentation durations as in the last 200 trials of Study 1, but still achieved fairly rapid presentation durations (capuchin mean = 112.35 ms; rhesus mean = 71.67 ms) while maintaining high levels of accuracy. However, despite the fact that by the last 200 trials both species were equally accurate, rhesus monkeys were initially more accurate than capuchin monkeys in Study 2. This shows that with experience, capuchin monkeys and rhesus monkeys were equally able to discriminate between similar (Asian language characters) and dissimilar (clip art) stimuli, but may indicate a slight species advantage in learning such visual processing skills for the rhesus monkeys. We should note however, that this is very likely at least in part due to the macaques competing more trials per session than the capuchins, which meant that they had an advantage in terms of achieving lower mean presentation durations in the last 200 trials.

Despite these similarities across species, within species there were performance differences across the studies. As mentioned above, capuchin monkeys did not reach as short of presentation durations in Study 2 as compared to Study 1, nor were they as accurate in the last 200 trials of Study 2 as compared to Study 1. Again, this may partially be due to the number of sessions it took the capuchins to complete 1000 trials, as presentation durations started over at 150 ms for each session. It is important to note that while their performance suffered in Study 2

as compared to Study 1, they still performed equally well compared to rhesus macaques. It is possible, therefore, that this was partially due to the fact that it took them more sessions to complete Study 2 (mean session = 2.9) than Study 1 (mean sessions = 2.4). While rhesus monkeys were more accurate in the first 200 trials of Study 1 as compared to Study 2, by the last 200 trials they were equally accurate in both studies. Thus while apparently logographic Asian language characters were initially more challenging for rhesus monkeys to discriminate than were clip art images, with experience they were equally well able to do both. As with capuchin monkeys, rhesus monkeys did not reach as short of presentation durations over the last 200 trials of Study 2 as they did with Study 1.

Comparing the data from this study to previous studies, we see that both capuchin monkeys and rhesus monkeys were able to correctly identify stimuli presented at durations so short that they are within the range of human perception without awareness (Bar & Biederman, 1998; Debner & Jacoby, 1994; Keysers et al., 2001). This suggests that rapid processing of visual information was selected for across the primate lineage. One interesting line of future research will be to investigate this across additional species to determine whether this ability is similar across the primates or instead reflects differences due to ecological pressures that differ between species. This may be particularly the case at very short processing durations. For example, gummivores may not require the same rapid processing abilities that would be adaptive in insectivores. We encourage more research to explore the lower bounds of this ability in primates, to see the ways in which this ability differs (or not) across the primates, and to explore inter-individual variation in non-human primate visual perception. Additionally, we encourage future research using rapid presentation durations to further explore these issues. For instance, we would like to test whether perception at these short durations occurs without awareness, as it does in humans (Bar & Biederman, 1998; Debner & Jacoby, 1994; Keysers et al., 2001). Additionally, we intentionally used ecologically irrelevant stimuli to avoid the confounds of stimuli that might carry high emotional valence (e.g., stimuli with rank or sex information). An obvious next step is to see how ecological relevance or emotional valence in stimuli influences processing speed and accuracy. Finally, it would be interesting to see the degree to which global versus local features of stimuli dominate at short presentation durations, or with different stimuli (*c.f.* Navon, 1977; Spinozzi, De Lillo, & Truppa, 2003). Exploring these and related questions in a variety of different primates will help to uncover both the selective pressures behind rapid visual processing seen in primates and the ways in which such abilities differ (or not) across the primate lineage.

References

- Bar, M., & Biederman, I. (1998). Subliminal visual priming. *Psychological Science*, *9*, 464-469.
- Bartz, A. E. (1962). Eye movement latency, duration, and response time as a function of angular displacement. *Journal of Experimental Psychology*, *64*, 318-324. doi: 10.1037/h0043475
- Cook, P., & Wilson, M. (2010). Do young chimpanzees have extraordinary working memory? *Psychonomic Bulletin & Review*, *17*, 599-600. doi: 10.3758/pbr.17.4.599
- D'Amato, M. R., & Worsham, R. W. (1972). Delayed matching in the capuchin monkey with brief sample durations. *Learning and Motivation*, *3*, 304-312. doi: 10.1016/0023-9690(72)90026-4
- Debner, J. A., & Jacoby, L. L. (1994). Unconscious perception: Attention, awareness, and control. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *20*, 304-317.
- Evans, T., Beran, M., Chan, B., Klein, E., & Menzel, C. (2008). An efficient computerized testing method for the capuchin monkey (*Cebus apella*): Adaptation of the LRC-CTS to a socially housed nonhuman primate species. *Behavior Research Methods*, *40*, 590-596. doi: 10.3758/brm.40.2.590

- Fragaszy, D., Visalberghi, E., & Fedigan, L. (2004). *The complete capuchin: The biology of the genus Cebus*. Cambridge, UK: Cambridge University Press.
- Inoue, S., & Matsuzawa, T. (2007). Working memory of numerals in chimpanzees. *Current Biology*, *17*, R1004-R1005. doi: 10.1016/j.cub.2007.10.027
- Keysers, C., Xiao, D.-K., Földiák, P., & Perrett, D. I. (2001). The speed of sight. *Journal of Cognitive Neuroscience*, *13*, 90-101. doi:10.1162/089892901564199
- Navon, D. (1977). Forest before trees: The precedence of global features in visual perception. *Cognitive Psychology*, *9*, 353-383.
- Orban, G. A. (2008). Higher order visual processing in macaque extrastriate cortex. *Physiological Reviews*, *88*, 59-89.
- Rilling, J. K., & Insel, T. R. (1999). The primate neocortex in comparative perspective using magnetic resonance imaging. *Journal of Human Evolution*, *37*, 191-223. doi: 10.1006/jhev.1999.0313
- Rumbaugh, D. M., Richardson, W., Washburn, D. A., Savage-Rumbaugh, E. S., & Hopkins, W. (1989). Rhesus monkeys (*Macaca mulatta*), video tasks, and implications for stimulus-response spatial contiguity. *Journal of Comparative Psychology*, *103*, 32-38.
- Spinozzi, G., De Lillo, C., & Truppa, V. (2003). Global and local processing of hierarchical visual stimuli in tufted capuchin monkeys (*Cebus apella*). *Journal of Comparative Psychology*, *117*, 15.
- Steiper, M. E., & Young, N. M. (2006). Primate molecular divergence dates. *Molecular Phylogenetics and Evolution*, *41*, 384-394.
- Truppa, V., Spinozzi, G., Stegagno, T., & Fagot, J. (2009). Picture processing in tufted capuchin monkeys (*Cebus apella*). *Behavioural Processes*, *82*, 140.
- Worsham, R. (1975). Temporal discrimination factors in the delayed matching-to-sample task in monkeys. *Learning & Behavior*, *3*, 93-97. doi: 10.3758/bf03209107