A competitive drive? Same-sex attentional preferences in capuchins

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In primates, faces provide information about several characteristics of social significance, including age, physical health, and biological sex. However, despite a growing literature on face processing and visual attention in a number of primate species, preferences for same- or opposite-sex faces have not yet been examined. In the current study, we explore the role of conspecific sex on visual attention in two groups of capuchin monkeys. Subjects were shown a series of image pairs on a Tobii Pro TX300 eye tracker, each depicting an unfamiliar male and an unfamiliar female face. Given the behavioral evidence of mate choice in both sexes, we hypothesized that capuchins would preferentially attend to images of unfamiliar conspecifics of the opposite sex. Our alternative hypothesis was that capuchins would preferentially attend to same-sex individuals to assess potential competitors. Our results provide support for our alternative hypothesis. When comparing attention to each stimuli type across sexes, females spent significantly larger percentages of time than males looking at female photos, whereas males spent significantly larger percentages of time than females looking at male photos. Within each sex, females looked for significantly larger percentages of time to female versus male images. Males also looked for larger percentages of time to same-sex images, though not significantly. To our knowledge, these data are the first to demonstrate significant sex-biased attentional preferences in adult primates of any species, and suggest that, for capuchins, potential competitors garner more attention than potential mates. In addition, our findings have implications for studies of visual attention and face processing across the primate order, and suggest that researchers need to control for these demographic factors in their experimental designs.

KEYWORDS
capuchin, eye tracking, face preferences, Sapajus [Cebus] apella, visual attention

1 | INTRODUCTION

Faces are a particularly important source of information for social species. In both human and nonhuman primates, faces can provide information about a myriad of characteristics of social significance, including age and physical health (e.g., Jones, Kramer, & Ward, 2012; Rhodes, 2006). In humans, faces also provide indicators of an individual’s biological sex, via differential characteristics in jawlines, cheekbones, and the relative prominence of brow bones (Thornhill & Moller, 1997). Both humans and nonhuman primates demonstrate the ability to distinguish male and female faces (e.g., humans: Bruce & Young, 1986; rhesus macaques [Macaca mulatta]: Koba & Izumi, 2006; chimpanzees [Pan troglodytes]: de Waal & Pokorny, 2008). However, very little is known about basic attentional preferences for same- or opposite-sex faces in nonhuman primates. Indeed, in a review of face processing in nonhuman primates, Parr (2011) stated...
that the sex of stimuli used is rarely reported but may influence face recognition performance. Given the increase in comparative approaches examining visual attention and face processing across the primate order (Leopold & Rhodes, 2010), it is critically important to determine whether demographic characteristics of the faces presented (such as biological sex) may bias attentional measures. Thus, in this contribution, we investigate whether male and female brown tufted capuchins (Sapajus apella, formerly Cebus apella) preferentially attend to unfamiliar faces of the same or opposite sex.

Human face perception and discrimination begin early in life. Within the first hours after birth, infants can discriminate between their mothers’ faces and unfamiliar faces (Bushnell, 2001), and this ability rapidly specializes to include discrimination between even unfamiliar male and female faces by 3 months of age (Quinn, Yahr, Kuhn, Slater, & Pascalis, 2002). The early ontogeny of face perception in the human infant is likely adaptive, as humans typically live in large social groups that require the recognition of thousands of faces (Haxby, Hoffman, & Gobbini, 2002; Sugden & Marquis, 2017). However, the selective pressures under which face perception and discrimination evolve are not unique to humans. Most nonhuman primates (hereafter: primates) live in complex social groups (Smuts, Cheney, Seyfarth, & Wrangham, 1987) wherein processing of facial information is likely of great importance (Byrne & Whiten, 1988; Reader & Laland, 2002). Evidence from neurological and behavioral research has highlighted the similarities in face processing and discrimination across a number of primate species. For example, functional magnetic resonance imaging studies comparing humans and rhesus macaques, an Old World monkey, show close anatomical correspondence in face-processing systems (e.g., Tsao, Moeller, & Freiwald, 2008). Similar results have been found in neural responses to faces in marmosets (Callithrix jacchus, a New World monkey; e.g., Hung et al., 2015) suggesting that a face-processing system common to all primates may have developed early in the course of primate evolution (Tsao et al., 2008). Parr (2011) reviewed both the similarities and differences in face processing between humans and monkeys and reported that research using passive viewing paradigms appear to result in more similarities than those using operant responses. In particular, several studies using pupil corneal reflection eye-tracking paradigms have demonstrated similarities in basic face-processing abilities across humans and primates. For example, adult rhesus monkeys individuate unfamiliar conspecific faces and perceive these faces in a holistic manner similar to humans (Dahl, Logothetis, & Hoffman, 2007), and adult great apes and humans evidence similar facial scan patterns (attending primarily to the eyes, mouth, and nose; Kano & Tomonaga, 2010).

In addition to basic discrimination amongst individuals, both humans and primates show attentional preferences for certain types of faces. In particular, human infants are attuned to the sex (male or female) of the faces they attend to from very early in life. For example, human infants prefer to attend to the sex of their primary caregiver, who is typically female (Quinn et al., 2002; Ramsey-Rennels & Langlois, 2006). This female face preference is also found in infant rhesus macaques, although it appears to wane across early development (Paukner, Huntsberry, & Suomi, 2010). In human heterosexual adults, several studies have reported evidence for an opposite- versus same-sex advantage in face processing (Cornwell et al., 2004; Kranz & Ishai, 2006; Perrett et al., 1998), which has been proposed to facilitate mate selection. However, preference for same- or opposite-sex faces is complicated by a variety of characteristics of both the displayed images (e.g., attractiveness, age, emotional valence, and social context) and the test subject (e.g., sexual orientation; reviewed in Proverbio, 2017; Rhodes, 2006). Much less is known about attentional preferences for same- or opposite-sex faces in primates. The majority of work that has been done thus far includes determining infant preferences for male or female faces (e.g., Paukner et al., 2010), examining the effect of estrus cycle on female preferences (e.g., Lacreuse, Martin-Malivel, Lange, & Herndon, 2007), or varying the characteristics of faces within one sex to measure preference for presumed indicators of fitness (e.g., symmetry: Paukner, Wooddell, Lefevre, Lonsdorf, & Lonsdorf, 2017; Waitt & Little, 2006; rank: Watson, Ghodasra, Furlong & Platt, 2011). Perhaps surprisingly, there have been no studies to our knowledge that simultaneously present images of conspecific faces of both sexes to examine sex-based visual preferences in adult primates. Therefore, other than infant macaques and humans, we know very little about preferences for same-sex or opposite-sex faces across the primate order.

Aside from great apes and rhesus macaques, the most common primate model for social cognition research is the capuchin. Although these New World monkeys are more distantly related to humans than the aforementioned taxa, they exhibit a suite of behaviors that underscores the importance of social information in their lives, including adept social learning abilities (Dindo, Thierry, & Whiten, 2008; Dindo, Whiten, & de Waal, 2009; Lonsdorf et al., 2016), complex social customs (Perry, 2011), and a bias for social information in memory (Howard, Festa, & Lonsdorf, 2018). Capuchin preferences for same- or opposite-sex faces has not been examined, but studies of their social behavior provide evidence for mate assessment and mate choice in both sexes which may suggest attentional biases toward the opposite-sex (i.e., potential mates). Capuchins live in mixed-sex social groups of 10–20 individuals that are characterized by a dominance hierarchy led by an alpha male (Izawa, 1980). In the wild, dispersal is male biased, but female dispersal, while more rare, has also been documented (Fragaszy, Visalberghi, & Fedigan, 2004). Agonistic behavior is more common among females than males, likely because low-ranking males tend to avoid more dominant males (Izawa, 1980). The mating system is multi-male/multi-female, and both males and females exhibit behaviors that are indicative of mate choice. Females in estrus typically court the alpha male by consistently following him and actively soliciting copulations (Carosi, Linn, & Visalberghi, 2005; Janson, 1984). What is unusual in capuchins when compared with other primates is that solicited males are initially reluctant to respond to female interest and may delay copulation for hours or days (Janson, 1984). Males eventually become receptive; however, they copulate infrequently (typically only once per day: Alfaro, 2005; Janson, 1984).
which has led some to suggest that limited male ejaculatory capacity selects for male mate choice. With regard to timing of copulations during a female’s proceptive phases (Alfaro, 2005). Direct male-male mating competition is relatively rare (Janson, 1986) and subordinate males typically employ alternative mating strategies (Alfaro, 2005).

With regard to face processing and attention to faces, Pokorny and de Waal (2009) demonstrated that capuchins discriminate pictures of familiar (in-group) and unfamiliar (out-group) conspecifics and therefore recognize the faces of groupmates from photographs. Talbot, Leverett, and Brosnan (2016) expanded on this study and found that capuchins distinguished between familiar members of a neighboring group and totally unfamiliar individuals. In this study, male subjects discriminated male faces better than female faces, whereas both male and female subjects discriminated female faces equally (Talbot et al., 2016). Similarly, Paukner et al. (2017) compared attentional preferences for facial symmetry in same- and opposite-sex conspecifics using videotaped looking time. In this paradigm, unaltered images of a conspecific were presented simultaneously with an image of the same individual that was altered to be symmetrical. Hence, only a single sex was presented at a time. The results showed that male capuchins preferentially attended to images of unfamiliar males that had been modified to be symmetrical, but females showed no preference for symmetry in either same- or opposite-sex conspecifics. The authors suggested that males may be more attentive to symmetrical faces as an indicator of male quality in the context of male-male competition.

Given the behavioral evidence of mate choice in both sexes, we hypothesized that adult capuchins would preferentially attend to images of unfamiliar conspecifics of the opposite sex as a form of mate assessment, as is seen in humans (Proverbio, 2017). Alternatively, capuchins may preferentially attend to same-sex individuals to assess potential competitors for mates or status (Paukner et al., 2017). To quantify attentional preferences, we used noninvasive eye-tracking methods and examined attention to paired same-sex and opposite-sex conspecific faces. Eye tracking has been increasingly used in a variety of contexts to explore attention in primates (e.g., Kano & Call, 2017; Kano, Call, & Tomonaga, 2012), including capuchins (Howard et al., 2018). Furthermore, the combination of preferential looking paradigms and eye-tracking devices has been used extensively in human infant research as a validated measure of both stimulus discrimination and preference (Aslin, 2007). This passive tracking method allows researchers to investigate attention with greater accuracy than that afforded by traditional looking time measures.

2 | METHODS

This study was approved by the Franklin & Marshall College IACUC. All methods were performed in accordance with the relevant guidelines and regulations of this committee and adhered to the American Society of Primatologists (ASP) Principles for the Ethical Treatment of Non-Human Primates. No modifications were made to standard animal care routines.

2.1 | Subjects and housing

We studied two colonies of adult brown capuchins living at the Franklin and Marshall College Vivarium (Lancaster, PA). Two individuals, one male, one female, were excluded from the study due to medical issues at the time of testing (male) or failure to voluntarily participate (female), leaving us with nine males (mean age = 16.7 years, range = 10–21.9 years) and eight females (mean age = 16.4 years, range = 8.2–38.1 years). Females were not tested when they were in estrus, given that previous work in nonhuman primates has found elevated responses to social stimuli during the estrus cycle (Lacreuse, Martin-Malivel, Lange, & Herndon, 2007, reviewed in Lacreuse, Mong, & Hara, 2015). Each colony lives in a main housing enclosure measuring approximately 3.35 m wide × 8.5 m long × 3.05 m high. Adjacent to each main enclosure is a wall of two rows of eight testing cubicles, each 0.91 m wide × 0.91 m long × 1 m high. The two colonies are separated by an observation room of one-way mirrored safety glass (see Lonsdorf et al., 2016 for a detailed schematic). Both colonies are maintained on a day/night light cycle, with light coming on gradually at 6 a.m. and going off gradually at 8 p.m. Meals of fresh produce and Mazuri Primate Diet (PMI Nutrition International, St. Louis, MO) are scattered once daily and other small quantities of cereal, fruit, nuts, and mealworms are provided during routine husbandry training and for enrichment.

2.2 | Apparatus and testing situation

For testing sessions, individual subjects were brought into testing cubicles from the main housing enclosure following standard positive reinforcement techniques. Eye gaze data were collected with a Tobii (Tobii Technology, Stockholm, Sweden) Pro TX300 pupil corneal reflection eye-tracking system (accuracy 0.4°, sampling rate 300 Hz) connected to a 23-inch TFT monitor (1,920 × 1,080 resolution). The tracking apparatus was placed on a mobile computer cart approximately 35 cm away from the testing cubic, allowing the monkey to voluntarily approach without interfering with the eye tracker. During test sessions, we either raised the plexiglass window of the testing cubic 2 inches so that subjects could look directly at the screen with no plexiglass barrier, or replaced the plexiglass with a large (2 × 1.5 in) wire mesh that they could look through to optimize collection of eye gaze data. These modifications were necessary because some of the testing cubicles had excessively scratched plexiglass windows that impeded gaze detection. There were no statistical differences between gaze collection rates using either method. We did not restrain the monkeys for testing; instead, we applied a small portion of peanut butter to the middle of the base of the testing window, such that the subjects could consume it while orienting toward the screen (similar to the provision of juice used in Kano & Call, 2014). Because we prioritized the ecological validity of this free access procedure, we were not able to standardize viewing distance. Thus, the viewing distance varied from approximately 35–70 cm depending on where in the testing cubic the monkeys were located during viewing. After initial eye gaze detection, the experimenter started the tracking
protocol then moved behind the cart and was obscured by a blind to prevent any attentional biasing. During testing sessions, the lights were dimmed to encourage attention to the monitor.

2.3 | Calibration

We collected and analyzed all data using the Tobii Studio software (version 3.4.8; Tobii Technology). Following previous work on unrestrained nonhuman subjects, we acquired a 9-point manual Tobii human eye calibration before testing (Howard et al., 2018; Howard, Wagner, Woodward, Ross, & Hopper, 2017). Given that calibration and recording accuracy increases with the number of points used (Tobii Technology, 2011), we used the highest number currently possible in the Tobii Studio system. This offline method of calibration was preferable in this case since capuchins have relatively short gaze fixations (Fragaszy, Deputte, Cooper, Colbert-White, & Mery, 2011) and were not restrained during testing, making sustained attention to the calibration dots rare. Furthermore, capuchin eyes are morphologically similar to human eyes (Franco, Finlay, Silveira, Yamada & Crowley, 2000; Montiani-Ferreira, Shaw, Mattos, Russ & Vilani, 2008; Silveira, Lee, Yamada, Kremers, & Hunt, 1998, 1999), suggesting that the eye model algorithms used for Tobii human calibration are suitable for capuchins. In addition, the suitability and accuracy of the offline human eye calibration procedure were confirmed directly by the Tobii development team (Tobii development team, personal communication, February 2019). The calibration process involved the presentation of a small animation depicting a lobster-like toy (approximately 5 × 5 cm, 188 × 188 pixels, 6° visual angle) accompanied by a short cartoon sound effect at each reference point. This animation was taken from the preloaded stimuli used in the Tobii Studio software for infant calibration. Post-hoc heat maps of capuchin gaze duration during testing were created in Tobii Studio to assess calibration accuracy in this paradigm (see Section 2.5).

2.4 | Data collection

During a testing session, each subject viewed a set of 10 image pairs. In each pair, the photos of faces of an unfamiliar male capuchin and unfamiliar female capuchin were presented on opposite sides of the screen (16.5 cm apart, 19° visual angle) for 10 s (Figure 1). Half of the trials presented a female face on the left side of the screen and a male on the right, and half of the trials presented a male face on the left side of the screen and a female on the right (see Figure 1). All images were of adult capuchin faces (5 years of age or older) gathered from other capuchin housing facilities, and in each picture the capuchin was shown looking straight ahead with a neutral expression. We took care to ensure that related individuals from

![Figure 1](image)

**FIGURE 1**  Example progression of three trials with stimulus presentations separated by attention-getter stimuli. The areas of interest used for analysis were drawn around the 10 × 10 cm images
other facilities were not included in the stimulus sets, so that all photos were of unfamiliar individuals. We standardized each image to $10 \times 10 \text{cm}$ (377 $\times$ 377 pixels, 11° visual angle) and included a naturalistic background for better ecological validity. We used Tobii Studio’s built in Latin Squares randomization feature to randomize the order of trials. Following each image pair presentation, a small focal point (a 5 $\times$ 5 cm picture of a toy lobster with a cartoon sound effect, 188 $\times$ 188 pixels, 6° visual angle) appeared in the center of the screen for 2 s, serving as both a calibration check and attention-getter (Morgante, Zolfaghari, & Johnson, 2012). The total length of stimulus presentation (the 10-image pair trials plus attention-getters) was 3 min and 45 s, after which subjects were released back into their main enclosure. On average, the total length of time that capuchins were in the cubicles for testing was 6 min.

As we did not restrain subjects during viewing, they would occasionally enter the testing cubicle but not orient toward the screen or disengage during testing. Therefore, we gave each subject up to three attempts to participate in the study. As such, we created three different stimulus sets that utilized the same capuchin face images, but varied the specific female/male image pairings across the 10 trials. If a subject attended for <1% of the time to the screen during any one participation attempt (as measured via the Tobii-generated sampling percentage), that data were not used in the final analysis, and they were rerun on a different test set at a later date, with at least 3 weeks in between attempts. The number of attempts required was: 1 attempt ($n$ = 7), 2 attempts ($n$ = 2), and 3 attempts ($n$ = 6).

2.5 Data analysis

To assess calibration accuracy, we utilized the Tobii Studio software to generate heat map visualizations (see Machado & Nelson, 2011, for an example with *M. mulatta*). These heat maps depicted both the distribution and duration of subject attention for the test trial photos and attention-getter stimuli (Figure 2). For visualization, we collapsed data across trials and participants for each of the three possible test sets, with the maps depicting absolute fixation duration (100 px radius). A visual inspection of the data found that subjects’ gaze was fixated roughly on the stimulus photos and attention-getting area, as opposed to the blank screen space between the picture boundaries.

Additionally, we exported fixation location data from Tobii Studio to examine the number of monkeys that attended to the $5 \times 5 \text{cm}$ (188 $\times$ 188 pixels, 6° visual angle) attention-getter between test trials. Out of 17 subjects, 12 demonstrated gaze fixations directly on the attention-getter, one provided gaze fixations 1.5 cm from the attention-getter (2° visual angle), and four did not provide gaze fixations to the attention-getter that were sufficient for analysis. The combined visual angle of the attention-getter (6°) plus the off-target visual angle provided by a single subject (2°) was smaller than the distance between stimulus pictures (16.5 cm apart, 19° visual angle), suggesting that the fixations captured were precise enough to be used for the current study. Taken together, these analyses demonstrate that the offline calibration was sufficient for the analysis of attention during our left/right visual preference task.

Based on the heat map data, we quantified attentional preferences in Tobii Studio by drawing areas of interest (AOIs) around each $10 \times 10 \text{cm}$ picture (male, female) in each trial, and summing looking duration (i.e., total fixation duration) to the male and female AOIs across all 10 trials. From these measures we quantified overall attention (in s) to male and female AOIs and to the screen overall, so that we could calculate the percent of time spent on each AOI (e.g., number of seconds looking at female AOIs/number of seconds looking at the screen).

We analyzed sex differences in visual attention both within and across sexes. First, we compared whether there were significant differences in percent of looking time to male and female photos between the sexes using the Mann–Whitney *U* test. Then, we used Wilcoxon’s signed rank tests to compare differences in looking time to same or opposite-sex individuals within each sex. We used two-tailed exact tests in all cases to determine test statistics and *p*-values, and set the $\alpha$ level at .05. We performed all analyses in Real Statistics Resource Pack software version 5.4 (Zaiontz, 2018).

3 RESULTS

We first conducted preliminary analyses to explore any effects of demographic characteristics on total looking time. We found no

![FIGURE 2](image-url)  Example heat map from one test set ($n$ = 6 subjects) of attention to the (a) test photos and (b) attention-getter, as a visualization of calibration accuracy. Red indicates the longest duration time, and green the least.
correlation between age and total looking time for either males or females, and no difference in looking times according to categorical dominance rank. Males looked to screen stimuli during test sessions for a significantly longer amount of time than females on average (males: mean ± standard deviation [SD] = 6.27 ± 4.38 s, n = 9, females: mean ± SD = 0.54 ± 0.34 s, n = 8; two-tailed exact Mann–Whitney U test: U = 4, p < .001). As such, we report all analyses comparing the sexes using the percentage of total looking time (e.g., looking to female faces/looking to screen stimuli) to control for these differences in raw looking times.

First, we examined the percent of time that male and female subjects attended to male and female images (Figure 3). Female capuchins spent significantly larger percentages of time than males looking at female images (females: mean ± SD = 53.14% ± 27.82%, n = 8, males: mean ± SD = 25.42% ± 10.68%, n = 9, two-tailed exact Mann–Whitney U test: U = 15, p = .008). In contrast, male capuchins spent significantly larger percentages of time than females looking at male images (males: mean ± SD = 37.46% ± 12.12%, n = 9, females: mean ± SD = 16.38% ± 20.22%, n = 8, two-tailed exact Mann–Whitney U test: U = 15, p = .036).

Within subjects and sexes, six out of eight females looked longer at female faces. On average, females looked longer to female faces (mean ± SD = 0.28 ± 0.17 s) versus male faces (mean ± SD = 0.1 ± 0.14 s; two-tailed exact Wilcoxon’s signed rank test: T = 2, n = 8, p = .046). Within males, seven out of nine males looked longer at male faces. However, while males looked longer on average to male (mean ± SD = 2.04 ± 1.24 s) versus female (mean ± SD = 1.62 ± 1.57 s) faces, this difference was not significant (two-tailed exact Wilcoxon’s signed rank test: T = 5, n = 9, p = .164).

4 | DISCUSSION

In this study, our aim was to examine preferential visual attention to same- or opposite-sex conspecific faces in capuchins. Given the increasing number of studies focusing on visual attention and/or face processing in primates (Leopold & Rhodes, 2010; Parr, 2011), it is surprising that this basic question has yet to be addressed. Based on behavioral evidence of mate choice in both male and female capuchins (Alfaro, 2005; Janson, 1984) we hypothesized that both sexes would prefer to look at photos of opposite-sex individuals. Alternatively, we hypothesized that capuchins would prefer to look at same-sex individuals as a form of competitor assessment. Using noninvasive eye-tracking methods, we found that females spent significantly larger percentages of time than males looking at female photos, whereas males spent significantly larger percentages of time than females looking at male photos (Figure 3). When examining looking time within each sex, we found that six out of eight female subjects preferred to look at photos of unfamiliar females when presented against photos of unfamiliar males, and looked for significantly longer durations at female photos. Males also showed a same-sex preference, in that seven of nine males preferred to look at photos of males, but the differences in duration of looking time were not significant. To our knowledge, this is the first study to demonstrate significant sex-biased attentional preferences in adult primates. Below, we interpret these findings with regard to capuchin social behavior and in terms of the broader consequences for studies of primate visual attention moving forward.

Capuchins live in large mixed-sex social groups led by an alpha male, who is the primary target of copulatory solicitations within a multi-male/multi-female mating system. Previous studies of facial recognition have demonstrated that capuchins can discriminate between members of their own group, a neighboring group, and totally unfamiliar individuals (Pokorny & de Waal, 2009; Talbot et al., 2016). In Talbot et al. (2016), male subjects discriminated male faces better than female faces, whereas both male and female subjects discriminated female faces equally, providing some of the first evidence of sex differences in visual processing in capuchins. However, while these findings speak to facial discrimination and processing abilities, they do not directly address preferences. In contrast, Paukner et al. (2017) explored whether capuchins preferred to attend to symmetrical versus asymmetrical conspecific faces, and found that male subjects looked significantly longer to symmetrical pictures of other males (but not females), though no such preference was found in female subjects. Taken together with the current study, the accumulating evidence shows that males discriminate other male faces better within an in-group/out-group paradigm (Talbot et al., 2016), preferentially look at more symmetrical males (Paukner et al., 2017), look for significantly higher percentages of time than females at images of unfamiliar male faces, and look for longer durations of time at images of unfamiliar male faces when presented simultaneously with unfamiliar female faces (this study). Thus, images of other males seem to be particularly salient for male capuchins, suggesting that male-male competition may have an important influence on visual attention in this species. These results are counter to our original hypothesis that capuchins would prefer to look at opposite-sex faces, and is somewhat puzzling given the relatively low levels of direct male-male competition within capuchin social groups (Janson, 1986). Within males, the percentage of time spent looking at unfamiliar males

\[\text{Percent of Total Looking Time}\]

\[\text{Female Subjects} \quad \text{Male Subjects}\]

\[\text{Female Faces} \quad \text{Male Faces}\]

**FIGURE 3** The average percent of looking time by male and female subjects to unfamiliar male or female faces (total seconds looking at image area of interest/total seconds looking to screen stimuli). Error bars denote standard error.
was higher than time spent looking at females, but not significantly so, which may represent the competing demands of intrasexual competition and mate assessment (Janson, 1986; Alfaro, 2005).

Our study also found consistent and significant visual preferences in female subjects toward female stimuli across all of our statistical comparisons. As mentioned above, agonistic interactions are more common among females (Izawa, 1980), and females actively attempt to disrupt copulations by aggressively targeting the female of the pair (Linn, Mase, Lafrancois, O’Keeffe & Lifshitz, 1995). Females are the primary initiators of copulations, which is manifested by persistent and aggressive pursuit and solicitations of the alpha male (Janson, 1986; Phillips, Bernstein, Dettmer, Devermann, & Powers, 1994). Thus, the preferential looking toward unfamiliar females we observed may be indicative of the primacy of competitor assessment over mate assessment. Female choice of males may be based less on visual assessment of facial characteristics and more on relative group-level social indicators, such as dominance status. A nonmutually exclusive possibility is that unfamiliar female faces are a relative novelty in capuchins, given that dispersal is male biased (though females can also disperse), and therefore garner more attention. However, unfamiliar male faces are also seen infrequently. Although sex-biased dispersal patterns are unlikely to be a proximate influence on visual attention in a captive group, these data suggest that the dispersal pattern of a particular species under study warrants consideration in future studies.

Males in our study looked for significantly longer than females overall, and there are several possible interpretations for this. As noted above, perhaps the competing demands of intra- and intersexual competition for males resulted in lengthier attention. It is also possible that males are simply more comfortable in the testing scenario itself (i.e., being separated from their social groups), but we did not note any substantial differences in behavioral responses, facial expressions or vocalizations during testing. Another possibility is that females are more averse to novel testing scenarios, but we have not found this to be the case in our subjects and in a wild study of responses to novel objects, females explored these significantly more than males (Visalberghi, Janson, & Agostini, 2003). Finally, it is important to note that, unlike many other primates, direct gaze in capuchins is not aversive, but rather is often used in the context of mating (see Fragaszy et al., 2004). Given that female capuchins are typically responsible for soliciting mating, and use direct gaze as part of this solicitation, we do not have any evidence that direct gaze in photos is particularly aversive for females. Future studies that incorporate both male and female subjects along with different types of image stimuli (e.g., social and nonsocial) would be helpful to distinguish among these possibilities.

Although the duration of time that our capuchins (especially females) looked at images appears relatively small, we contend that this does not negate the value of these findings. Capuchins have relatively short gaze fixations (i.e., <1 s), even for more complex tasks that involve direct human interaction (Fragaszy et al., 2011). However, in Fragaszy et al. (2011), even 1 s of attention was sufficient to shift capuchin subjects’ attention to the experimental objects used by a human demonstrator in a novel object-action matching paradigm. In addition, our gaze durations are similar to those found in Howard et al. (2018) for capuchins looking to familiar versus novel block towers, where an effect of the type of model (social vs. nonsocial) on memory was detectable. In chimpanzees, a visual presentation of 210 ms was sufficient for subjects to be able to correctly remember a sequence of nine stimuli (Inoue & Matsuzawa, 2007). Although none of these tasks exactly matches the paradigm presented here, they support our contention that we should not negate the importance of small gaze durations. Instead, we argue that as more primate (and nonprimate) species are studied using eye tracking in naturalistic and/or free access testing scenarios, we will have a much greater understanding of the speed with which primates can gain information from visual stimuli.

As this is the first study exploring sex-based attentional preferences in adult primates, it is still unknown how these preferences might change with subject age and social context. Previous studies of sex-biases in human and macaque infants have found preferences for female faces though research suggests that these preferences attenuate over early development (Paukner et al., 2010; Quinn et al., 2002). In contrast, human adults typically prefer opposite-sex faces (Proverbio, 2017), suggesting changes in human preferences across development. As the existing data on primates encompasses macaque infants (Paukner et al., 2010; Parr et al., 2016; Paukner, Stonecker, Murphy, Wooddell, & Dettmer, 2018) and adult capuchins (this study), we are currently unable to determine how these preferences change across life stages in any primate species. A longitudinal and/or cross-sectional approach within a particular species that documents changes across infancy, at puberty, and into adulthood is an important focus for future studies. In addition, comparative approaches across species with different social organizations and levels of intra- and intersexual competition would allow us to more fully explore how visual preferences are influenced by social dynamics.

Finally, our results suggest that future researchers should take care to control for the sex of individuals presented as stimuli, and that previously published studies may need to be re-examined taking sex of the subject stimuli into account. As noted by Parr (2011), sex of the image subject is rarely reported in studies of primate face processing, but could influence the outcomes of such studies in significant ways. For example, in a recent report on chimpanzees’ abilities to discriminate other primate species (gorilla, orangutan, baboon, capuchin, and human), sex of the subject stimuli was not reported despite significant sexual dimorphism in some of the species examined, and only female test subjects were used (Wilson & Tomonaga, ). Our understanding of sex differences in visual attention and processing in primates is in its infancy, and we urge researchers to incorporate both demographic characteristics (e.g., sex and age) and social experience (e.g., captive rearing history: Paukner et al., 2018; Tanaka, 2007) into their experimental designs. The integration of these factors, along with careful consideration of species-typical social dynamics, will lead to a richer and more ecologically valid understanding of primate visual attention, preferences and processing.
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