Behavioural Processes 124 (2016) 38–46

Contents lists available at ScienceDirect

Behavioural Processes

journal homepage: www.elsevier.com/locate/behavproc

Using photographs to study animal social cognition and behaviour: Do capuchins' responses to photos reflect reality?

F. Blake Morton[a,b,*], Sarah F. Brosnan[c], Laurent Prétôt[c], Hannah M. Buchanan-Smith[a,b], Eoin O'Sullivan[a,b], Martina Stocker[d], Daniel D'Mello[a], Vanessa A.D. Wilson[b,e]

[a] Behaviour and Evolution Research Group, Psychology, School of Natural Sciences, University of Stirling, UK
[b] Scottish Primate Research Group, UK
[c] Department of Psychology and Language Research Center, Georgia State University, GA, USA
[d] Department of Cognitive Biology, University of Vienna, Austria
[e] Department of Psychology, University of Edinburgh, UK

ARTICLE INFO

Article history:
Received 21 April 2015
Received in revised form 30 August 2015
Accepted 9 October 2015
Available online 22 October 2015

Keywords:
Brown capuchin monkey
Sapajus apella
Ecological validity
Image
Social decision-making
Visual media
Visual perception

ABSTRACT

Behavioural responses to photos are often used to infer what animals understand about their social environment, but are rarely validated against the same stimuli in real life. If subjects' responses to photos do not reflect responses to the same live stimuli, it is difficult to conclude what happens in reality based on photo responses alone. We compared capuchins' responses to photos versus live stimuli in an identical scenario within research cubicles. Subjects had the opportunity to approach food placed in front of an alpha group member and, in a separate condition, photos depicting the same individual. Subjects' latencies to approach food when placed in front of the real alpha negatively correlated with time subjects spent in close proximity to the alpha in their main enclosure. We therefore predicted subjects' latencies to approach food in the presence of photos would positively correlate with their latencies to approach food in the presence of the real alpha inside the cubicles, but negatively correlate with time they spent in proximity to the alpha in their enclosure. Neither prediction was supported. While not necessarily surprising, we explain why these results should be an important reminder that care is needed when interpreting results from photo studies.

© 2015 Elsevier B.V. All rights reserved.

1. Introduction

Visual media are widely used to study animal social cognition and behaviour, particularly how animals perceive, understand, and respond to social information (Bovet and Vauclair, 2000; Fagot and Parron, 2010; Fagot et al., 2010). For instance, researchers may record subjects' responses to photos or videos depicting social situations (e.g. the face of a familiar group member, or the perinea of a sexually receptive female; Bovet and Vauclair, 2000; Schell et al., 2011). Photos are particularly favoured among researchers because they are easier than videos to manipulate and control for specific variables (e.g. colour saturation, size/shape; Rowland and Perrett, 1995), can be manipulated in a realistic fashion (e.g. placing photos in a location where the real animal might be found), and allow researchers to explore subjects' responses to individuals or situations that would otherwise be difficult or impossible to recreate naturally.

Throughout the literature, animals' responses to photos, such as their spontaneous reactions (e.g. facial expressions, eye gaze) or their ability to discriminate and categorise social content (e.g. familiar versus unfamiliar, kin versus non-kin), have been used to explore animals' reactions to social stimuli in controlled ways (reviewed in Bovet and Vauclair, 2000). These data are often interpreted as being socially meaningful. For example, baboons (*Papio hamadryas*) gaze longer at images of conspecifics' eyes compared to images of their mouths and noses, suggesting that the eyes are the most salient feature of faces for this species (Kyes and Candland, 1987). European starlings (*Sturnus vulgaris*) and domesticated sheep (*Ovis aries*) respond less fearfully and more affiliatively to images of conspecifics compared to controls (e.g. photos of humans and landscapes), suggesting that they process and are attracted to the social content of those images (Vandenheede and Bouissou 1994, 1995; Perret et al., 2015). Finally, dogs are able to discriminate between photos of happy versus angry faces of

* Corresponding author at: Psychology, School of Natural Sciences, University of Stirling, Stirling FK9 4LA, UK.
E-mail address: Morton.blake@gmail.com (F.B. Morton).

http://dx.doi.org/10.1016/j.beproc.2015.10.005
0376-6357/© 2015 Elsevier B.V. All rights reserved.

humans, suggesting that they are sensitive to humans' emotional states (Müller et al., 2015).

In many of these cases, we can learn quite a lot from photos. For instance, if an animal discriminates from photos certain individuals better than others (e.g. known versus unknown individuals), or focuses on a particular feature of photos (e.g. the eyes), it can help researchers identify what aspects of those stimuli are most salient to the animal. Although we still may not know how the animal interpreted the photos, the fact that they can, for instance, discriminate a photo of a known individual better than that of a stranger at least tells us that they better recognize familiar individuals. Even if they are using non-social cues (e.g. colour preference; D'Amato and Van Sant, 1988), it may be that they are also using the same cues in real life to make those discriminations.

Nevertheless, using photos to specifically understand social cognition and behaviour based on responses to photos alone is challenging. If subjects do not react to an image as they would a real animal, then the results do not necessarily tell us anything about what happens in reality. As such, results can be more ambiguous without comparing subjects' responses to the same live stimuli as a baseline. For example, in cases of spontaneous reactions to photos, a male subject may be curious or confused about a "frozen" image of a female conspecific, and therefore spend more time exploring or gazing at that image; yet, the same response could also be interpreted as a sign of sexual attraction—as is often the case in studies of primates (e.g. Griffey, 2011; Pflüger et al., 2014; Waitt et al., 2003; Waitt and Little, 2006). Given the absence of other sensory cues (noise, smell, movement), there also remains the possibility that subjects treat social content in photos as inanimate features of "objects" rather than depictions of socially-relevant stimuli, which, under certain experimental paradigms (e.g. where spontaneous reactions are recorded), might affect an animal's decision-making on the task, or their motivation to attend to certain features of the stimuli. Therefore, establishing whether subjects' responses to photos reflect their responses to the same stimuli in real life can help researchers address these concerns.

Researchers very rarely compare animals' responses to photos to the same stimuli in real life. For some experimental paradigms, e.g. in cases where photos are digitally manipulated, this may not be feasible. However, when it is possible to do so, such a comparison may be a useful tool for interpreting the social relevance of subjects' responses to photos, particularly where the assumption is that behavioural reactions to photos are equivalent to their reactions to the same, live stimuli (e.g. testing hypotheses about mate choice preferences; Griffey, 2011; Waitt et al., 2003; Waitt and Little, 2006). If subjects respond to photos as they do towards the same live stimuli, it supports the notion that subjects treat photos as they do in reality; meaning, behavioural reactions to images may tell us something about subjects' perception and understanding of live social stimuli. If, however, subjects' responses to photos do not reflect how they respond to the same stimuli in real life, it suggests that it may not be safe to assume those responses reflect subjects' real-life social behaviour and/or socio-cognitive skills. In such instances, results must be interpreted with caution. For studies that require the use of images, it may be beneficial to include more sophisticated forms of experimentation, such as fMRI analyses to identify neural mechanisms, to help interpret the data.

We tested whether brown capuchin monkeys (*Sapajus* sp., formerly *Cebus apella*; Alfaro et al., 2012) would react to social stimuli (depicted in photos) as they would the same, live stimuli. Researchers often use "floating faces", i.e. an image of a face with no body, to test social perception in animals (Bovet and Vauclair, 2000; Guo et al., 2003; Pokorny and de Waal, 2009; Griffey, 2011), but full body images may provide stronger social cues and are the only direct comparison to a real animal. We therefore gave our subjects the opportunity to approach or avoid food placed in front of either a floating face (i.e. a cut-out colour photo of a face without a body) or a full body image (i.e. life-size, cut-out colour photo) of an alpha member of their own group. Most studies utilizing images rely on a computerized presentation in which the images depict animals in locations that real animals never inhabit (e.g. on a computer screen outside the animal's enclosure). This makes a direct comparison between photos and real stimuli impossible. Therefore, in the current study, we presented cut-out printed images of the alpha to subjects within research cubicles, which enabled us to test subjects individually under controlled conditions, but in a location where they were accustomed to seeing real conspecifics (i.e. other members of their group). Subjects' responses to the images were then compared to their latencies to approach food when the real alpha (the same individual depicted in photos) was inside an adjacent cubicle, and the total amount of time subjects spent in close proximity to the real alpha within their group's main indoor/outdoor enclosure (i.e. a natural, non-experimental context). Wild and captive studies of brown capuchins have shown that relatively lower-ranking individuals often avoid close proximity to higher-ranking group members, presumably to avoid aggression (e.g. Fragaszy et al., 2004; Janson, 1990; Morton, 2014). We therefore predicted that subjects' latencies to approach food in the presence of photos would be positively related to their latencies to approach food when the real alpha was inside the cubicles. We also predicted that subjects' responses to photos within the cubicles would be negatively related to the amount of time they spent in close proximity to the real alpha in their main enclosure.

2. Methods and materials

2.1. Study sites and subjects

There were eighteen subjects from two sites. Five juveniles (between 1 and 4 years old; Fragaszy et al., 2004) and six adults (>4 years old) were housed at the "Living Links to Human Evolution" Research Center (LL), UK (Leonardi et al., 2010; MacDonald and Whiten, 2011). Age of these study subjects ranged from 2.29 to 8.17 years for males (average 4.81 ± SD 2.01 years, $N = 8$ capuchins), and 5.63 to 13.28 years for females (average 9.68 ± SD 3.85 years, $N = 3$ capuchins). The other seven monkeys were adults, and housed at the Language Research Center (LRC) of Georgia State University, USA. Age of these study subjects ranged from 7 to 11 years for males (average 9.3 ± SD 2.08 years, $N = 3$ capuchins), and 12 to 18 years for females (average 15.25 ± SD 3.2 years, $N = 4$ capuchins). Further details on group composition and animal husbandry at each site are provided in Section 2.1 of the Supplementary electronic materials.

2.1.1. Subjects' prior experience with photos

At LL, four adults participated in a study by Griffey (2011), which took place in 2010 and involved presenting subjects with photos of the faces of unfamiliar capuchins. One of these adults (Kato) was also the subject of an eye-tracking study in November, 2012, whereby he was exposed to photos of unfamiliar and familiar group members (Living Links, unpub. data). At the LRC, all subjects had prior experience with a facial discrimination study using photos of the faces of familiar and unfamiliar conspecifics, which took place between February and November, 2013 (one female was still participating in the facial discrimination study at the time of testing for this study). All of the previous studies at both sites displayed photos on computer screens (i.e. pixelated glowing images) and photos were not to scale. Subjects had never before seen printed photos of conspecifics nor full body photos like those used in the present study (Section 2.3). Subjects also had never before been exposed to photos placed inside the research cubicles where testing for this study took place.

Table 1
Summary of each experimental photo condition administered to the Living Links (LL) and Language Research Center (LRC) monkeys.

Experimental condition	Description	Study location
Face-Direct	Floating face with direct eye gaze	LL
Full Body-Direct	Full body with direct eye gaze	LL
Face-Averted	Floating face with averted eye gaze	LL and LRC
Full Body-Averted	Full body with averted eye gaze	LL and LRC
Real Monkey	Real monkey in adjacent cubicle	LL

2.1.2. Ethical standards

Subjects' participation in this study was entirely voluntary; they were able to access the research cubicles via a corridor connecting the cubicles to their main enclosure. This study was approved by Living Links, the IACUC of Georgia State University, and complied with regulations of the Association for the Study of Animal Behaviour (ASAB, 2012).

2.2. Photos of monkeys

Subjects were presented with photos of an alpha monkey from their group. Alpha status was determined based on behavioural observations including wariness of other group members, how much aggression individuals received, how many fights individuals won versus lost, whether they were being sought out for mating, how many offspring they sired/gave birth to, their level of assertive behaviour (e.g. manipulative, bold, aggressive) relative to others, how often they received and gave grooming to others, and their ability to take food from humans and other monkeys (see Fragaszy et al., 2004; Lefevre et al., 2014; Morton et al., 2013; Morton, 2014). The combination of these traits allow for easy and straight-forward recognition of alpha status among our capuchins. Lefevre et al. (2014) reported complete inter-rater agreement for alpha status assignment for the monkeys used in our study, using raters with at least one year of experience working with the monkeys from their site.

All photos were taken within six months prior to testing, and depicted each monkey's face angled towards the camera (Section 2.2 in the Supplementary electronic materials). The Face-Direct and Full Body-Direct conditions used photos depicting the alpha monkey's eyes gazing into the camera, while the Face-Averted and Full Body-Averted conditions used photos depicting an averted gaze (Table 1; Section 2.3). Within each group of monkeys, the same test subjects were all exposed to photos of the same alpha individual. Photos were printed in colour on xerox paper to reduce glare from light and mounted on stiff cardboard to avoid bending during the study. All photos were life-size, which was estimated visually while the monkeys were inside the research cubicles.

2.3. Experimental conditions

There were five experimental conditions (Table 1). At LL, the Face-Direct and Full Body-Direct conditions preceded the Face-Averted and Full Body-Averted conditions. Therefore, the Face-Averted and Full Body-Averted conditions were replicated at the LRC to address the possibility that the LL monkeys' responses to these conditions were affected by their recent exposure to the Face-Direct and Full Body-Direct conditions (e.g. habituation to photos). The LRC subjects did not undergo the Face-Direct and Full Body-Direct conditions since the sole purpose of their involvement was to replicate the Face-Averted and Full Body-Averted conditions among a sample of capuchins that was naïve to the study.

The Face-Direct and Face-Averted conditions tested capuchins' responses to photos depicting a "floating face"; that is, a life-size colour image of the alpha's face with no body, displayed on a plain piece of white 21 × 29.7 cm paper (Fig. 1a). At LL, the photo and paper was always taped to the far end of cubicle B at the capuchins' eye level. At the LRC, the photo and paper was attached to a wooden stand located 5 cm from the far end of cubicle B, in the same location as stimuli used in training and to administer the Full Body-Averted condition.

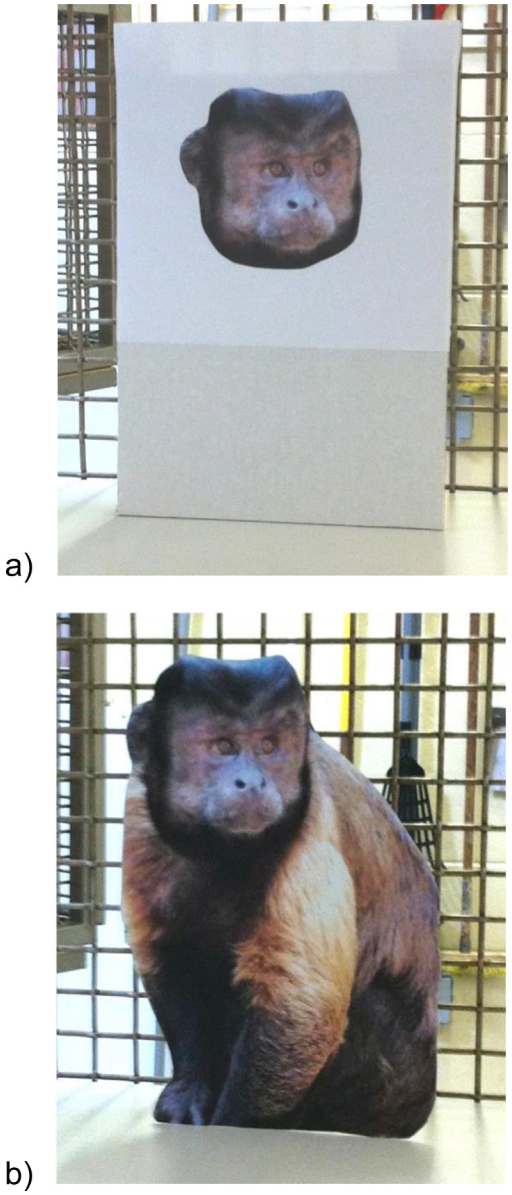

Fig. 1. Example of (a) a floating face glued to a white sheet of paper and (b) a full body photo from the LRC.

The Full Body-Direct and Full Body-Averted conditions tested subjects' responses to photos of the same alpha monkey shown to them in the other photo conditions, but depicting a full body image; that is, a life-size, cut-out colour image of the individual, with full body and no background (Fig. 1b). The cut-out photo was glued to cardboard using non-scented glue, and placed upright on a small wooden stand (not visible to the subject) inside the test cubicle to give the impression that the monkey was sitting inside the cubicle. The photo was approximately 5 cm behind the food reward.

2.4. Setup

Training and testing took place inside research cubicles. Each subject was tested individually. All training/testing trials lasted for

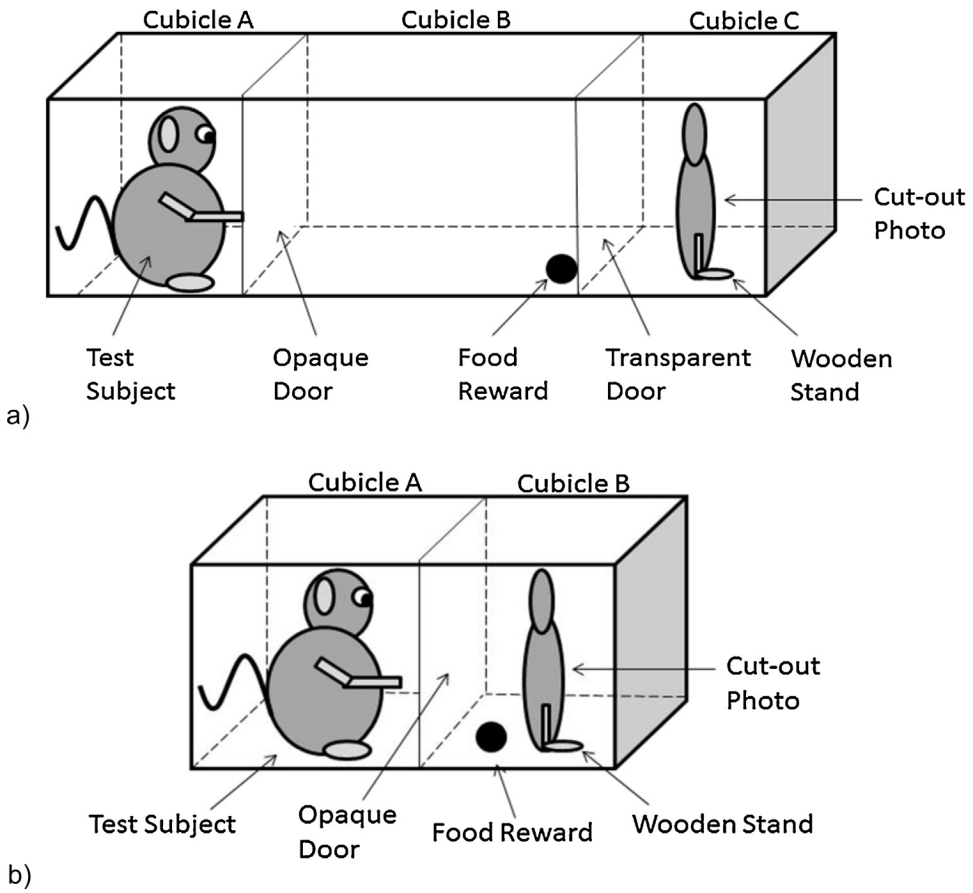

Fig. 2. Illustration of the experimental setup involving a full body photo administered to monkeys at (a) Living Links and (b) the Language Research Center.

one minute (or up to five minutes at the LRC), or until subjects made physical contact with the food reward. At no point during this study did any subject end testing prematurely (e.g. by gesturing to the cubicle door exit).

Fig. 2a depicts the general setup at LL. The heights and widths of cubicles A–C were exactly the same (52.1 cm × 51.4 cm); however, the middle cubicle (cubicle B) was twice the length of cubicles A and C (cubicle B: 99 cm; cubicle A/C: 49.5 cm). An opaque Plexiglas sliding door separated cubicles A and B, while a transparent sliding door separated cubicles B and C. During training and experimental trials, a subject was closed inside cubicle A. Then, a researcher would open the opaque door leading into cubicle B, which contained a highly-preferred food reward—a cluster of approximately six raisins.

Fig. 2b depicts the general setup at the LRC. Cubicles A and B had the same dimensions (71.12 cm in width × 71.12 cm in length × 60.96 cm in height), and were separated by an opaque Plexiglas sliding door. Similar to the LL setup, during training and experimental trials the LRC subjects were closed inside cubicle A. Then, a researcher would open the opaque door leading into cubicle B, which contained a highly preferred food reward (i.e. one full small grape or half a big grape).

At both sites, care was taken to ensure that subjects were paying attention and standing at the door leading into cubicle B, i.e. waiting to enter the cubicle, before the researcher opened it. During all training and experimental trials, subjects were allowed to enter cubicle B and freely take the food reward. No other food was given to the subject until the end of the trial. All non-participating subjects were kept out of the testing area so they would not have any exposure to the setup prior to their own test.

2.5. Training

2.5.1. Living Links

Training at LL took place between 30 September and 14 October, 2013. In preliminary runs, it was estimated that it would take subjects approximately 2–3 s to walk (at a normal pace) from cubicle A to cubicle C. Therefore, subjects underwent at least one training trial per day until their minimum latency to obtain food rewards was approximately 3 s for three consecutive trials. In all trials, a plain sheet of white paper (21 cm × 29.7 cm) was taped to the middle of the door of cubicle B and C, on the cubicle C side. Food rewards were placed on the floor of cubicle B, approximately 5 cm in front of the paper. The purpose of the white paper was to habituate subjects to the presence of a "foreign object" within the cubicles prior to tests involving floating face images, which also had a white background (Section 2.3; Fig. 1a).

2.5.2. Language Research Center

Training at the LRC took place between 5 and 12 April, 2014, and was similar to the LL setup (Fig. 2b). In preliminary runs, it was estimated that it would take subjects approximately 2 s to walk (at a normal pace) from cubicle A to cubicle B. The shorter times here were due to the smaller size of the testing area compared to those at LL. Subjects underwent at least one training trial per day until their minimum latency to obtain food rewards remained approximately 2 s for three consecutive trials. As at LL, training was done with a white piece of paper in the same location as the photos used for testing; the paper was mounted on a wooden stand located approximately 5 cm from the far side of the testing chamber.

2.6. Testing

Subjects underwent each experimental condition only once. At LL, testing took place between 8 and 28 October, 2013. Conditions were counterbalanced across testing days such that no more than half the subjects received the same condition on the same day, and each monkey underwent no more than two conditions on the same day.

At the LRC, testing took place between 14 and 15 April, 2014. Conditions were counterbalanced and subjects were tested only once per day on each condition.

2.7. Measuring latencies to take food rewards

Sessions were video recorded at both sites; latencies were also recorded in real time. To test for inter-observer reliabilities, an independent observer coded 25% of the video data from each site, and these codings were compared to the latency measurements recorded in real time for the same exact trials. "Latency to obtain food" was defined as the time in seconds it took for the subject to make physical contact with the food reward (e.g. touch with mouth or hand) after the door separating cubicles A and B began to slide open. In all trials, the experimenter opened the door in approximately 1 s. Subjects' latencies during their last trial of training were used as a "control" condition (i.e. after subjects were fully trained, but before any experimental stimuli were presented) to compare to subjects' responses to each experimental condition; the control condition would indicate whether subjects were reacting to each photo stimulus.

2.8. Measuring behaviour towards the real alpha monkey

Using scan sampling methods (Martin and Bateson, 2007), spatial proximity data were recorded at each site within each group's main indoor/outdoor enclosure approximately six weeks prior to the start of subjects' training. At LL, behavioural observations were made between 9 and 18 h from 23 August to 3 October, 2013, with three samples taken each day. At the LRC, behavioural observations were made between 8:30 and 9 h from 28 January to 10 March, 2014, and samples were recorded every three minutes over 30 min, for a total of 11 samples each week. Any monkey located within one body length of the sampled individual was identified and noted. At LL, a total of 92 scans were collected for the East group, and 89 for the West group. At the LRC, a total of 110 scans were collected for Griffin's group and 88 scans were collected for Gabe's group. All monkeys were sampled equally at both sites. Individual scores were calculated for each monkey by summing the total number of samples in which subjects spent in close proximity to the alpha monkey depicted in the photos.

2.8.1. Validation of the spatial proximity measures

To establish whether spatial proximity was a relevant behaviour to compare with subjects' latencies in conditions involving photos, monkeys at LL underwent a single trial (Real Monkey condition; Table 1) during which they were required to obtain food when the real alpha monkey was sitting inside cubicle C. Testing took place between 11 and 21 October, 2013, and was counter balanced with the Face-Direct and Full Body-Direct conditions.

2.9. Statistical analyses

Pearson correlations were used to test for inter-observer reliabilities in measuring subjects' latencies to approach food. Correlation coefficients $r > 0.9$ were defined as high inter-observer reliability.

Bootstrapped *t*-tests were used to test for significant differences in subjects' latencies to approach food between training and experimental conditions (Table 1). To reduce the risk of capitalizing on Type 1 error inflation due to our multiple comparisons, we also ran one-way ANOVA tests between conditions using a post hoc Bonferroni correction.

To investigate possible age-related differences in photo perception (e.g. Schell et al., 2011), bootstrapped Pearson correlations were used to test for significant associations between age (in years) and subjects' latencies to approach food in each photo condition. Bonferroni corrections were applied to significant results. Age-related analyses were only necessary for the LL subjects since the LRC subjects were all adults.

Bootstrapped Pearson correlations were used to test associations between subjects' latencies to obtain food in all photo conditions and the Real Monkey condition, and between photo conditions and the amount of time subjects spent in close proximity to the real alpha in their main enclosure. Bonferroni corrections were applied to significant results. Significant differences between the *r*-values for conditions involving full body and floating face images were determined using Fisher's *z*-tests.

Fisher's *z*-tests were conducted in R (version 3.0.1). All other analyses were conducted using SPSS 21.0 (SPSS, IBM Corp., Chicago, USA). Analyses involving each photo condition were conducted with and without including monkeys with prior photo experience (Section 2.1). For all bootstrapped analyses, 95% confidence intervals (CI) were generated (with replacement = 10,000) using the bias-corrected and accelerated bootstrap (Efron 1987; Davison and Hinkley, 1997).

3. Results

3.1. Inter-observer reliability tests

Latency measurements were highly concordant between the blind observer and the researchers who coded the video data (LL video: $r = 0.98$, $P < 0.001$, $N = 20$ trials; LRC video: $r = 0.99$, $P < 0.001$, $N = 14$ trials). Thus, latency measurements were considered reliable at both sites.

3.2. Validation of the spatial proximity measures

Subjects' latencies to obtain food in the Real Monkey condition (Table 1) were negatively correlated with the amount of time they spent in close proximity to the alpha within their main enclosure ($r = -0.65$, bootstrapped 95% CI = [−0.77, −0.65], $N = 11$); meaning, subjects who spent less time in close proximity to the alpha also took longer to approach food when the alpha was inside the cubicles. Thus, the spatial proximity data were considered a behaviourally valid measure to compare with monkeys' latencies to obtain food in the presence of each photo stimuli (Table 1).

3.3. Differences in latencies between training and experimental photo conditions

The LL subjects underwent an average of 6 ± SD 1.10 training trials in which no photo stimuli were presented. Average latency to obtain food rewards during the final trial of training was 2.18 ± SD 0.75 s. During testing with photos, subjects' average latency to obtain food rewards was 4.50 ± SD 2.54 s in the Face-Direct condition (i.e. floating face with direct eye gaze), 9.54 ± SD 6.0 s in the Full Body-Direct condition (full body photo with direct eye gaze), 2.05 ± SD 0.91 s in the Face-Averted condition (floating face with averted gaze), 2.86 ± SD 0.89 s in the Full Body-Averted condition (full body photo with averted gaze), and 10.45 ± SD 17.11 s in the Real Monkey condition (i.e. the real alpha in an adjacent cubicle).

Table 2
Age-related effects on subjects' responses to photo stimuli.

	Pearson correlations[a]	
	r	95% CI[b]
Face-Direct condition	−0.192	[−0.751, 0.773]
Full Body-Direct condition	−0.29	[−0.77, 0.463]
Face-Averted condition	−0.063	[−0.691, 0.866]
Full Body-Averted condition	−0.128	[−0.691, 0.329]

[a] Pearson correlations between the LL subjects' ages (in years) and their responses to photo stimuli in each condition.
[b] Bias-corrected and accelerated bootstrapped 95% confidence intervals (CI).

Age did not correlate with subjects' responses to each photo condition (Table 2). Compared to subjects' final training session (i.e. the controlled condition), subjects exhibited on average significantly longer latencies to obtain food rewards in the Face-Direct condition ($t = -3.14$, df = 10, bootstrapped 95% CI = [−4.15, −0.59]), Full Body-Direct condition (t = −3.99, df = 10, bootstrapped 95% CI = [−11.18, −4.09]), the Real Monkey condition ($t = -1.63$, df = 10, boot- strapped 95% CI = [−18.64, −1.18]), the Full Body-Averted condition ($t = -2.68$, df = 10, bootstrapped 95% CI = [−1.18, −0.23]), but not in the Face-Averted condition ($t = 0.38$, df = 10, bootstrapped 95% CI = [−0.68, 0.86]). Mean latencies in the Face-Direct condition were significantly shorter than those in the Full Body-Direct condition ($t = -2.57$, df = 10, bootstrapped 95% CI = [−9.70, −1.64]), but significantly longer compared to the Face-Averted condition ($t = 3.75$, df = 10, bootstrapped 95% CI = [1.41, 3.82]) and the Full Body-Averted condition ($t = 2.41$, df = 10, bootstrapped 95% CI = [0.55, 3.09]). Latencies in the Face-Direct condition were significantly shorter than those in the Real Monkey condition (t = −1.63, df = 10, bootstrapped 95% CI = [−19.67, −1.45]). Latencies in the Full Body-Direct condition were significantly shorter than those in the Real Monkey condition ($t = -1.51$, df = 10, bootstrapped 95% CI = [−19.76, −0.77]). Latencies in the Full Body-Direct condition did not significantly differ from those in the Real Monkey condition ($t = -0.17$, df = 20, bootstrapped 95% CI = [−15.32, 8.49]). A one-way ANOVA with Bonferroni correction revealed a significant difference in monkeys' latencies to approach food across conditions ($F(5,60) = 2.80$, $P = 0.03$). Compared to subjects' final training session, subjects exhibited on average significantly longer latencies to obtain food rewards in the Face-Direct condition (mean difference = −2.32, bootstrapped 95% CI = [−3.88, −0.83]), the Full Body-Direct condition (mean difference = −7.36, bootstrapped 95% CI = [−11.24, −3.88]), and the Real Monkey condition (mean difference = −8.27, bootstrapped 95% CI = [−21.02, −0.71]), but not in the Face-Averted condition (mean difference = 0.14, bootstrapped 95% CI = [−0.59, 0.89]) or the Full Body-Averted condition (mean difference = −0.68, bootstrapped 95% CI = [−1.36, 0.03]) (Fig. 3a). Mean latencies in the Face-Direct condition were significantly shorter compared to those in the Full Body-Direct condition (mean difference = −5.05, bootstrapped 95% CI = [−9.14, −1.55]), and significantly higher compared to the Face-Averted condition (mean difference = 2.46, bootstrapped 95% CI = [1.05, 4.02]) and the Full Body-Direct condition (mean difference = 1.64, bootstrapped 95% CI = [0.22, 3.15]). Latencies in the Face-Direct condition did not significantly differ from those in the Real Monkey condition (mean difference = −5.95, bootstrapped 95% CI = [−18.92, 1.76]). Latencies in the Full Body-Direct condition did not differ significantly from those in the Real Monkey condition (mean difference = −0.91, bootstrapped 95% CI = [−14.88, 8.31]). Latencies in the Face-Averted condition did not significantly differ from those in the Full Body-Averted condition (mean difference = 0.82, bootstrapped 95% CI = [−0.01, 1.61]).

At the LRC, subjects underwent four training trials; average latency to obtain food rewards during the final trial of

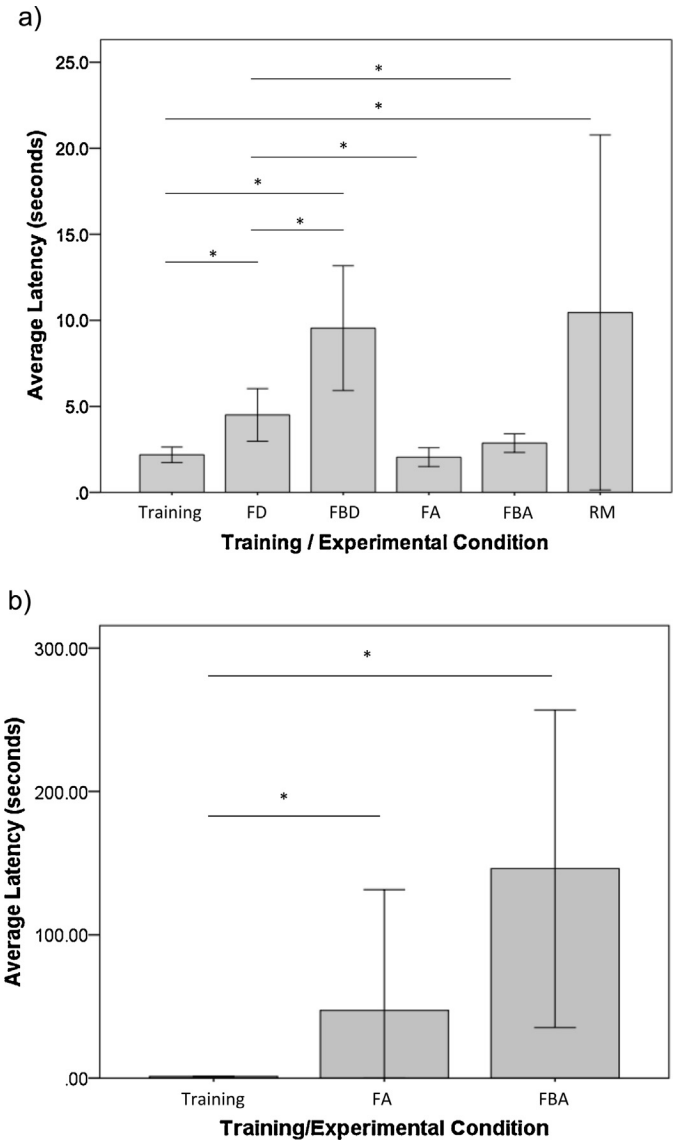

Fig. 3. Average latencies to obtain food rewards in training and experimental conditions among the (a) Living Links monkeys and (b) LRC monkeys. FD—floating face with direct eye gaze, FBD—full body photo with direct eye gaze, FA—floating face with averted eye gaze, FBA—full body with averted eye gaze. *—Statistically significant based on a 95% CI bootstrapped one-way ANOVA with Bonferroni correction. Error bars represent standard errors from the mean.

training was 1.09 ± SD 0.17 s. Subjects' average latency to obtain food was 47.26 ± SD 111.53 s in the Face-Averted condition, and 146.12 ± SD 146.51 s in the Full Body-Averted condition. Compared to subjects' final training session (i.e. the control condition), subjects exhibited on average significantly longer latencies to obtain food rewards in the Face-Averted condition ($t = -1.10$, df = 6, bootstrapped 95% CI = [−132.87, −1.08]) and the Full Body-Averted condition ($t = -2.62$, df = 6, bootstrapped 95% CI = [−256.81, −45.43]), respectively. Latencies in the Full Body-Averted condition were significantly longer than those in the Face-Averted condition ($t = -1.89$, df = 6, bootstrapped 95% CI = [−183.22, −12.83]). A one-way ANOVA with Bonferroni correction revealed a non-significant trend in differences between monkeys' latencies to approach food in each condition ($F(2,18) = 3.40$, $P = 0.06$). Compared to subjects' final training session, subjects showed significantly longer latencies to obtain food rewards in the Face-Averted condition (mean difference = −46.17, bootstrapped 95% CI = [−152.97, −1.13]) and the Full Body-Averted condition (mean difference = −145.04,

Table 3
Correlations between LL subjects' responses to each photo condition and real monkey conditions.

	Real Monkey condition[a]		Spatial proximity[b]	
	r	95% CI[c]	*r*	95% CI[c]
Face-Direct condition	0.173	[−0.365, 0.845]	−0.249	[−0.751, 0.756]
Full Body-Direct condition	0.149	[−0.449, 0.848]	−0.454	[−0.885, 0.418]
Face-Averted condition	0.147	[−0.532, 0.821]	−0.352	[−0.84, 0.505]
Full Body-Averted condition	0.573	[−0.01, 0.883]	−0.485	[−0.856, 0.45]

[a] Pearson correlations between the LL subjects' latencies to approach stimuli in photo conditions and their latencies in the real monkey cubicle condition.
[b] Pearson correlations between the LL subjects' latencies to approach stimuli in photo conditions and time spent in close proximity to alpha in main enclosure.
[c] Bias-corrected and accelerated bootstrapped 95% confidence intervals (CI).

bootstrapped 95% CI = [−249.95, −37.94]); however, latencies in the Face-Averted condition did not significantly differ from those in the Full Body-Averted condition (mean difference = −98.86, bootstrapped 95% CI = [−220.89, 27.67]) (Fig. 3b).

3.4. Responses to photos versus real monkeys

At LL, subjects' latencies in photo conditions were not significantly related to their latencies to approach food in the Real Monkey condition nor the amount of time individuals spent in close proximity to the alpha within their main indoor/outdoor enclosure (Table 3). Correlation coefficients did not differ significantly between the Face-Direct and Full Body-Direct conditions ($z = 0.46$, $P = 0.65$), and between the Face-Averted and Full Body-Averted conditions ($z = 0.34$, $P = 0.73$). For all analyses, significance did not change when the four monkeys with prior photo experience were excluded (Table 1 in the Supplementary electronic materials).

At the LRC, the amount of time subjects spent in close proximity to the alpha within their main enclosure was not significantly related to subjects' latencies in the Face-Averted condition ($r = 0.10$, bootstrapped 95% CI: [−0.69, 0.99]) or in the Full Body-Averted condition ($r = -0.47$, bootstrapped 95% CI: [−0.93, 0.03]). The correlation coefficients from the Face-Averted and Full Body-Averted conditions did not significantly differ ($z = 0.85$, $P = 0.40$).

4. Discussion and conclusions

Questions about the ecological validity of using photos to study animal cognition and behaviour have already been reviewed in previous work (e.g. Fagot and Parron, 2010; Fagot et al., 2010; Bovet and Vauclair, 2000; Waitt and Buchanan-Smith, 2006). Our study, however, provides a rare test of the ecological validity of these methods by comparing subjects' behavioural reactions to social content depicted in photos with their behaviour towards the same social stimuli in real life. Contrary to our predictions, capuchins' responses to photos did not reflect their behaviour towards the real stimuli.

As previously discussed, wild and captive studies of brown capuchins show that relatively lower-ranking individuals often avoid close proximity to higher-ranking group members, presumably to avoid aggression (e.g. Fragaszy et al., 2004; Janson, 1990; Morton, 2014). This is particularly true in competitive situations, such as instances where two or more individuals are presented with a potentially monopolizable food source (as in the present study). The purpose of our testing whether latency to approach food was reflective of proximity to the alpha in the monkeys' main enclosures served only to demonstrate the behavioral validity of the measure, and thereby confirm what previous studies have already reported for alpha-subordinate capuchin relationships. Subjects' latencies to approach food inside the research cubicles when in the presence of the real alpha were negatively correlated with the amount of time subjects spent in close proximity to those individuals within their social group, i.e. a natural non-experimental setting. These results are consistent with previous work on wild and captive capuchins. Thus, while subjects at LL may have perceived the Plexiglas doors of the cubicles as a protective barrier to the photo stimuli and real monkey conditions (which were all placed in adjacent cubicles), latency to approach food inside the cubicles was an ecologically valid behaviour to compare with data on spatial proximity within their main enclosure.

Excluding monkeys with prior photo experience had no effect on the significance of the results and, as previously discussed, the experimental design of this study was completely novel to all subjects (Section 2.1). There were also no age-related differences in juveniles' and adults' responses to photos. Therefore, prior photo experience and developmental differences in photo perception cannot explain our results (e.g. Rosenfeld and Van Hoesen, 1979; Schell et al., 2011).

At LL, subjects' responses in the Face-Direct were shorter compared to their responses to the Full Body-Direct condition. Also, at the LRC, subjects responses to the Face-Averted condition were shorter compared to their responses to the Full Body-Averted condition. Such findings may be due to the fact that the floating face conditions were considerably smaller. Capuchins may have approached the full body conditions more slowly possibly because they were acting more cautious and/or were more curious or distracted by the larger stimuli. Regardless of why, however, capuchins may have needed more time to process the visual information in front of them, hence why they showed longer latencies to approach the food reward in those conditions.

At LL, subjects' responses in the Face-Direct and Full Body-Direct conditions differed significantly from their responses to the Face-Averted and Full Body-Averted conditions. One possibility is that, like most Old World primates, direct eye gaze is perceived as a threatening gesture among capuchins, and therefore the capuchins of our study showed longer latencies to approach photo conditions with direct eye gaze compared to photos with averted eye gaze. Alternatively, the monkeys may have quickly become habituated to photos with repeated exposure (see Fagot and Parron, 2010; Rosenfeld and Van Hoesen, 1979), which could have affected the LL monkeys' latencies during the Face-Averted and Full Body-Averted conditions (which were presented to them after the Face-Direct and Full Body-Direct conditions). Nevertheless, regardless of the underlying reason for these results, the LRC subjects were only presented with the Face-Averted and Full Body-Averted conditions, yet they did not respond to photos as they did towards the same individuals in real life. Therefore, any possible effects of habituation are unlikely to have affected our ability to test the main hypotheses of this study.

The angle between the observer and each test subject meant that we could not always determine the exact time when subjects first made visual contact with the photos, which may have affected our latency calculations. However, it seems unlikely, albeit not entirely possible to rule out, that the monkeys did not detect the photos upon entering the cubicles. For one, experimenters waited until subjects were looking in the direction of cubicle B before opening the door. Second, monkeys were trained prior to testing so they knew where to look for food in the cubicle (which we placed near each photo). Lastly, based on eye gaze and head angle, it was clear that in all trials, subjects were viewing the general direction of the photos as they approached the food. A large, conspicuous and novel object placed in close proximity to the food would very likely have captured their attention.

Several reasons might explain why the capuchins in this study did not respond to the stimuli in photos in the same way as they did to real life animals. The most obvious reason is that in the absence of other sensory cues like noise, movement, and smell,

subjects were fully aware that the photos were not real and thus did not respond to them as such. Second, our subjects may have been deterred by the photo stimuli. There is a phenomenon in both humans and other primates called the "uncanny valley," in which subjects respond with notable aversion to stimuli that are too lifelike (Mori, 1970; Steckenfinger and Ghazanfar, 2009). It is possible that in our effort to create extremely lifelike images, we inadvertently created images that were perplexing or off-putting. The fact that subjects' latencies were substantial in the case of full body images may indicate that this effect, or something like it, influenced our results. Third, of course, it is possible that there is something fundamentally different about how capuchins process photos compared to real conspecifics, which could explain why our subjects had very different behavioural reactions to images compared to the real animals. This is perhaps the most troubling conclusion and, for reasons already discussed (Section 1), should be an important reminder that care is needed when interpreting animals' responses to photos. For example, Fagot et al. (2010) propose three levels of pictorial processing in animals: (1) confusion (i.e. the animal responds to the photo as if it were real), (2) independence (i.e. the animal makes no connection between the image and its content), and (3) equivalence (i.e. the photo is "read" as a representation of its referent, but is not perceived as the real thing). As noted previously, capuchins appear capable of recognizing conspecifics in photos (Pokorny and de Waal, 2009), and therefore are unlikely to perceive photos independent of their content. Also, since our study subjects did not respond to photos as if they were real individuals, it suggests that photos do not elicit a confusion response in these animals. Although further research is needed, these findings collectively suggest that capuchins may process photos under an "equivalence" mode as defined by Fagot et al. (2010) (see also Truppa et al., 2009), and therefore did not treat them as "real animals".

The purpose of replicating the Face-Averted and Full Body-Averted conditions with the LRC monkeys was to test our hypotheses involving these conditions within a sample of monkeys who were completely naïve to the study and its methods. In other words, due to possible order effects at Living Links, by replicating these conditions (which were administered to the LL monkeys after the Face-Direct and Full Body-Direct conditions) we could test our hypotheses in the relative absence of any bias due to order effects. While indeed site differences in variables like subjects' age, housing condition, relationship quality toward their group's alpha, and prior experience with photos may underlie the observed differences found between the LL and LRC monkeys' responses to the Face-Averted and Full Body-Averted conditions, our main point remains: If monkeys (in general) respond to photos in a way that reflects how they respond to the same stimuli in real life, then monkeys from both sites should have done so. This was not the case in the present study, and only furthers our argument that it is essential that researchers remain cautious when interpreting the behavioural and cognitive underpinnings of their animal subjects' responses to photos.

4.1. Future directions

Photos may enable researchers to identify particular aspects of animal social cognition and behaviour that would otherwise be difficult to test in real life, particularly natural settings. For example, in the case of primate eye gaze, lower-ranking individuals may not have the opportunity or the willingness to closely study the face of an alpha due to the associated risks (i.e. conflict from direct eye gaze; Hauser, 1996; van Hoof, 1967). However, based on our example, we believe that it is very important to use caution when interpreting the social relevance of such results since it is unclear what aspects of photo stimuli those animals are using when deciding how to behave. As previously discussed, it is rare for researchers to compare subjects' responses to photos with the same stimuli in real life. Further work is therefore needed to determine how animals interpret the social content of photo stimuli.

It would be interesting to test whether monkeys are more likely to respond to photos as they would live stimuli when exposed to a less or non-competitive situation. Capuchins likely rely on using social cues to gauge whether or not they should approach an alpha group member, and as we already have discussed, the lack of certain cues in photos (e.g. movement, smell) may result in different behavioural responses compared to when the real individual is present. This may not be the case in a non-competitive situation, where the subjects may not be as concerned or as focused on the movements and eye gaze of the alpha. Testing a similar set of conditions in a less competitive context could potentially result in different findings related to similarities and differences between photos and real stimuli.

An important limitation to our study is that with only a small number of participants in this study, statistical power may have been too low to detect significant differences between subjects' responses to photos and their responses to the same stimuli in real life. We attempted to reduce this risk by bootstrapping our analyses (Brownstone and Valletta, 2001). However, due to the low sample size, and the fact that this study was conducted on a single nonhuman primate species, our study should only serve as a stepping-stone for future studies to discuss and improve upon. We strongly encourage further work using a larger sample of participants, ideally covering a range of species that differ in their sensory perception (e.g. birds, dogs, rodents, primates).

Printed photo stimuli were used in this study in an attempt to provide a direct comparison to our real monkey condition within the cubicles. We encourage further work on a broader range of experimental conditions, particularly computerized presentation, which are commonly used by researchers but rarely placed in "realistic" locations (e.g. on a table placed outside the testing cubicle).

Although our study focused specifically on photos, we encourage similar work on other types of visual media, particularly videos. Unlike photos, videos are of course more realistic in terms of their depiction of motion and sound, which in turn may increase their ecological validity to test subjects. For instance, Shimizu (1998) found that male rock doves (*Columba livia*) respond to videos of female conspecifics using similar displays compared to their behaviour towards the same females in real life. Collectively, we look forward to future work that will highlight the best ways of using visual media technology to study animal social behaviour and cognition.

Conflict of interest

All authors declare no conflicts of interest.

Acknowledgements

We thank Prof. Andrew Whiten, Director of Living Links, for permission to conduct research at this facility, and to all of the staff for their support and assistance, particularly Lara Wood, Alison Dowling, and Sophie Pearson. We are especially grateful to RZSS Edinburgh Zoo for permission to work within the zoo. We thank Catherine Talbot for providing photos from the LRC, Lauren Robinson and Kelly Leverett for coding video for inter-observer reliability testing, and Kelly Leverett for completing the behavioural observations at the LRC. We are grateful to Valentina Truppa, Laura Wood, Sophia Daoudi, and the anonymous reviewers for providing useful comments on earlier drafts.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.beproc.2015.10.005.

References

Alfaro, J.W.L., E Silva Jr., J.S., Rylands, A.B., 2012. How different are robust and gracile capuchin monkeys? An argument for the use of *Sapajus* and *Cebus*. Am. J. Primatol., http://dx.doi.org/10.1002/ajp.22007.

ASAB, 2012. Guidelines for the treatment of animals in behavioural research and teaching. Anim. Behav. 83, 301–309.

Bovet, D., Vauclair, J., 2000. Picture recognition in animals and humans. Behav. Brain Res. 109, 143–165.

Brownstone, D., Valletta, R., 2001. The bootstrap and multiple imputations: harnessing increased computing power for improved statistical tests. J. Econ. Perspect. 15, 129–141.

D'Amato, M.R., Van Sant, P., 1988. The person concept in monkeys (*Cebus apella*). J. Exp. Psychol.: Anim. Behav. Processes 14, 43–55.

Davison, A.C., Hinkley, D.V., 1997. Bootstrap Methods and Their Applications. Cambridge University Press, Cambridge, ISBN 0-521-57391-2.

Efron, B., 1987. Better bootstrap confidence intervals. J. Am. Stat. Assoc. 82 (397), 171–185, http://dx.doi.org/10.2307/2289144.

Fagot, J., Parron, C., 2010. Picture perception in birds: perspective from primatologists. Comp. Cogn. Behav. Rev. 5, 132–135.

Fagot, J., Thompson, R.K.R., Parron, C., 2010. How to read a picture: lessons from nonhuman primates. PNAS 107 (2), 519–520.

Fragaszy, D.M., Visalberghi, E., Fedigan, L.M., 2004. The Complete Capuchin: The Biology of the Genus *Cebus*. Cambridge University Press, New York, NY.

Griffey, 2011. Human and non-human primate preferences for faces and facial attractiveness. In: PhD Thesis. University of Stirling, UK.

Guo, K., Robertson, R.G., Mahmoodi, S., Tadmor Young, M.P., 2003. How do monkeys view faces?—a study of eye movements. Exp. Brain Res. 150, 363–374.

Hauser, M.D., 1996. The Evolution of Communication. MIT Press, Cambridge, MA.

Janson, C.H., 1990. Social correlates of individual spatial choice in foraging groups of brown capuchin monkeys, *Cebus apella*. Anim. Behav. 40, 910–921.

Kyes, R.C., Candland, D.K., 1987. Baboon (*Papio hamadryas*) visual preference for regions of the face. J. Comp. Psychol. 101, 345–348.

Lefevre, C.E., Wilson, V.A.D., Morton, F.B., Brosnan, S.F., Paukner, A., Bates, T.C., 2014. Facial width-to-height ratio relates to alpha status and assertive personality in capuchin monkeys. PLoS One, http://dx.doi.org/10.1371/journal.pone.0093369.

Leonardi, R., Buchanan-Smith, H.M., Dufour, V., MacDonald, C., Whiten, A., 2010. Living together: behavior and welfare in single and mixed species groups of capuchin (*Cebus apella*) and squirrel monkeys (*Saimiri sciureus*). Am. J. Primatol. 72, 33–47.

MacDonald, C., Whiten, A., 2011. The 'Living Links to Human Evolution' research centre in Edinburgh zoo: a new endeavour in collaboration. Int. Zoo Yearb. 45, 7–17.

Martin, P., Bateson, P., 2007. Measuring Behaviour: An Introductory Guide. Cambridge University Press, Cambridge, UK, http://dx.doi.org/10.1017/CBO9780511810893.

Mori, M., 1970. The uncanny valley. Energy 7, 33–35.

Morton, F.B., 2014. Individual differences in learning, personality, and social success in brown capuchin monkeys (Sapajus sp.). Doctoral thesis submitted to the University of Stirling, UK. http://dspace.stir.ac.uk/handle/1893/21886?mode=full#.Vlh-FoQiolI.

Morton, F.B., Lee, P.C., Buchanan-Smith, H.M., Brosnan, S.F., Thierry, B., Paukner, A., de Waal, F.B., Widness, J., Essler, J.L., Weiss, A., 2013. Personality structure in brown capuchin monkeys (*Sapajus apella*): comparisons with chimpanzees (*Pan troglodytes*), orangutans (*Pongo* spp.), and rhesus macaques (*Macaca mulatta*). J. Comp. Psychol. 127, 282–298.

Müller, C.A., Schmitt, K., Barber, A.L.A., Huber, L., 2015. Dogs can discriminate emotional expressions of human faces. Curr. Biol. 25, 601–605.

Perret, A., Henry, L., Coulon, M., Caudal, J.-P., Richard, J.-P., Cousillas, H., Hausberger, M., George, I., 2015. Social visual contact, a primary drive for social animals? Anim. Cogn., http://dx.doi.org/10.1007/s10071-015-0834-8.

Pflüger, L.S., Valuch, C., Gutleb, D.R., Ansorge, U., Wallner, B., 2014. Colour and contrast of female faces: attraction of attention and its dependence on male hormone status in *Macaca fuscata*. Anim. Behav. 94, 61–71.

Pokorny, J.J., de Waal, F.B.M., 2009. Monkeys recognize the faces of group mates in photographs. PNAS 106 (51), 21539–21543.

Rosenfeld, S.A., Van Hoesen, G.W., 1979. Face recognition in the rhesus monkey. Neuropsychologia 17, 503–509.

Rowland, D.A., Perrett, D.I., 1995. Manipulating facial appearances through shape and color. IEEE Comput. Graph. Appl. 15 (5), 70–76.

Schell, A., Rieck, K., Schell, K., Hammerschmidt, K., Fischer, J., 2011. Adult but not juvenile *Barbary macaques* spontaneously recognize group member from pictures. Anim. Cogn. 14, 503–509.

Shimizu, T., 1998. Conspecific recognition in pigeons (*Columbia libia*) using dynamic video images. Behaviour 135, 43–53.

Steckenfinger, S.A., Ghazanfar, A.A., 2009. Monkey visual behavior falls into the uncanny valley. PNAS 106 (43), 18362–18366.

Truppa, V., Spinozzi, G., Stegagno, T., Fagot, J., 2009. Picture processing in tufted capuchin monkeys (*Cebus apella*). Behav. Processes 82, 140–152.

van Hoof, J.A.R.A.M., 1967. The facial displays for the catarrhine monkeys and apes. In: Morris, D. (Ed.), Primate Ethology. Aldine Publishing Company, Chicago, pp. 7–68.

Vandenheede, M., Bouissou, M.F., 1994. Fear reactions of ewes to photographic images. Behav. Processes 32, 17–28.

Vandenheede, M., Bouissou, M.F., 1995. Fear reactions of domestic sheep confronted with either a human or a human-like model. Behav. Processes 34, 81–92.

Waitt, C., Buchanan-Smith, H.M., 2006. Perceptual considerations in the use of colored photographic and video stimuli to study nonhuman primate behavior. Am. J. Primatol. 68, 1054–1067.

Waitt, C., Little, A.C., 2006. Preferences for symmetry in conspecific facial shape among *Macaca mulatta*. Int. J. Primatol. 27 (1), 133–145.

Waitt, C., Little, A.C., Wolfensohn, S., Honess, P., Brown, A.P., Buchanan-Smith, H., Perrett, D.I., 2003. Evidence from rhesus macaques suggests that male coloration plays a role in female mate choice. Biol. Lett., http://dx.doi.org/10.1098/rsbl.2003.0065.