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

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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.

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

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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.