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Original Article

Extraneous color affects female macaques' gaze preference for photographs of male conspecifics☆

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ABSTRACT

Humans find members of the opposite sex more attractive when their image is spatially associated with the color red. This effect even occurs when the red color is not on the skin or clothing (i.e. is extraneous). We hypothesize that this *extraneous color effect* could be at least partially explained by a low-level and biologically innate generalization process, and so similar extraneous color effects should be observed in non-humans. To test this possibility, we examined the influence of extraneous color in rhesus macaques (*Macaca mulatta*). Across two experiments, we determined the influence of extraneous red on viewing preferences (assessed by looking time) in free-ranging rhesus monkeys. We presented male and female monkeys with black and white photographs of the hindquarters of same and opposite sex conspecifics on either a red (experimental condition) or blue (control condition) background. As a secondary control, we also presented neutral stimuli (photographs of seashells) on red and blue backgrounds. We found that female monkeys looked longer at a picture of a male scrotum, but not a seashell, on a red background (Experiment 1), while males showed no bias. Neither male nor female monkeys showed an effect of color on looking time for female hindquarters or seashells (Experiment 2). The finding for females viewing males suggests that extraneous color affects preferences among rhesus macaques. Further, it raises the possibility that evolutionary processes gave rise to extraneous color effects during human evolution.

1. Introduction

Body ornaments and bright colors may be selected through sexual selection for their ability to indicate elements of quality or condition to conspecifics (Darwin, 1872). Species as diverse as mandrills (*Mandrillus sphinx*: Setchell, 2005), red junglefowl (*Gallus gallus*: Zuk et al., 1990), and two-spotted goby fish (*Gobiusculus flavenscens*: Amundsen & Forsgren, 2001) make use of such sexual signals. The form that signals take may originate from sensory biases, which are imperfections in psychological templates for other important environmental elements (e.g. brightly colored foods like fruits and flowers: Arak & Enquist, 1993; Dawkins & Guilford, 1996; Endler & Basolo, 1998). These imperfections, and the signal recipient's tendency to respond, can be exploited by conspecific traits that advertise quality or condition, and over evolutionary time, further preferences and elaborations of those traits can result in a sexual signal. Thus, unorthodox stimuli that replicate some aspects of the original sexual signal can reveal sensory biases.

Consistent with this idea, some animals exhibit greater attraction to others in the presence of a color even when it is not a natural part of the body (Arak & Enquist, 1993). For example, several bird species exhibit preferences for opposite sex conspecifics that have artificial leg bands of the appropriate color (e.g. zebra finches *Taeniopygia guttata*: Burley, Krantzberg, & Radman, 1982; Hunt, Cuthill, Swaddle, & Bennett, 1997; double-bar finches *Poephila bichenovii*: Burley, 1986; American goldfinches *Carduelis tristis*: Johnson, Dalton, & Burley, 1993; Bluethroats *Luscinia svecica*: Johnsen, Lifjeld, & Rohde, 1997). Similarly, uncrested zebra finches show preferences for individuals to whom white crests (but not those of any other color) have been experimentally added (Burley & Symanski, 1998). These examples demonstrate that a receiver can have a generalized template for the signal they seek, which can be exploited under unusual or unnatural circumstances that mimic some aspects of the original signal.

The sensory bias concept may apply to a known red-attraction association in humans. Research indicates that humans are particularly attracted to individuals displaying or in close proximity to the color red. Increased facial redness is perceived as more attractive

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(Re, Whitehead, Xiao, & Perrett, 2011; Stephen, Oldham, Perrett, & Barton, 2012) and individuals wearing red are considered more attractive and sexually desirable (Elliot & Niesta, 2008; Gueguen, 2012; Roberts, Owens, & Havilcek, 2010). Even extraneous red (i.e., red not on skin or clothing) has an effect, as men and women rate black and white photographs of opposite sex individuals framed in red as more attractive and sexually desirable (Elliot et al., 2010; Schwarz & Singer, 2012). In humans, the red effect could reflect cultural influences. Indeed, in many cultures red is linked to sex and romance, and red may enhance attraction entirely due to learned associations (Elliot & Maier, 2012; Hutchings, 2004). However, as the human phenomenon resembles sensory biases for colors in non-humans, such effects could also have biological roots.

Whether human and animal color-attraction effects are derived from similar evolutionary processes is unclear. Non-natural cues in birds do not produce effects in some instances (zebra finches: Ratcliffe & Boag, 1987; bluethroats: Johnsen, Fiske, Amundsen, Lifjeld, & Rohde, 2000); one possible reason is that these color biases do not extend beyond manipulations of the original mate or require natural contexts (Hunt et al., 1997). The aim of the present research was to test for the extraneous color effect observed in humans in a non-human primate, using a method matched as closely as possible to that used in human studies. Documenting such an effect would provide evidence that responses to extraneous colors in mating contexts may have similar biological roots across species, including humans.

Here, we measured rhesus macaques' looking time as a proxy for interest in or preference for black and white photographs of the scrota/hindquarters of opposite sex conspecifics overlaid on a red or blue background (Fig. 1a). Both male and female rhesus macaques use red body signals in sexual displays. Mating season brings a redder scrotum to males, and redder hindquarters and faces to both sexes, but little or no sexual swelling (Baulu, 1976). Female facial coloration darkens around ovulation (Higham et al., 2010) and attracts the attention of males (Higham et al., 2011; Waitt, Gerald, & Little, 2006). While the correlation of male coloration with male condition remains unclear (Higham, Pfefferle, Heisterman, Maestripieri, & Stevens, 2013), experimental manipulations have also suggested that females are attracted to artificially reddened male faces (Waitt et al., 2003). If these sexual signals of male and female rhesus macaques have evolved from, or have led to the evolution of, a more generalized sensory bias, then unorthodox stimuli that contain aspects of the signal – in this case black and white photographs of conspecifics on a red background – should still elicit greater interest in that image, as measured in increased looking-time, in opposite sex macaques. The absence of such a result would be indicated by similar looking-times across conditions, regardless of stimulus content.

2. Experiment 1: males and females viewing male scrota

2.1. Methods

2.1.1. Subjects

We tested rhesus macaques (*Macaca mulatta*) from the semi-provisioned free-ranging population of approximately 1000 monkeys at the Cayo Santiago field site in Puerto Rico. These monkeys are well studied and habituated to human observation (Rawlins & Kessler, 1986). Their conditions are semi-natural, living in naturally formed social groups, but about 50% of their diet is provisioned monkey chow (Rawlins & Kessler, 1986). Individuals are identifiable by tattoos and ear notches and complete records on individual ages are maintained. This research with this population was approved by the Institutional Animal Care and Use Committee at the University of Puerto Rico and was therefore in compliance with ethical animal use rules and laws.

We completed a full session – four trials – with 56 subjects (29 female, 27 male) for this experiment. We approached 78 additional subjects but they did not complete a session due to subject inattention, movement toward or away from the apparatus, or interference from other monkeys. We did not include individuals that did not complete a full session in the data analysis. This failure rate (55%) is typical for field studies with this population using very similar methods (e.g. Cheries,

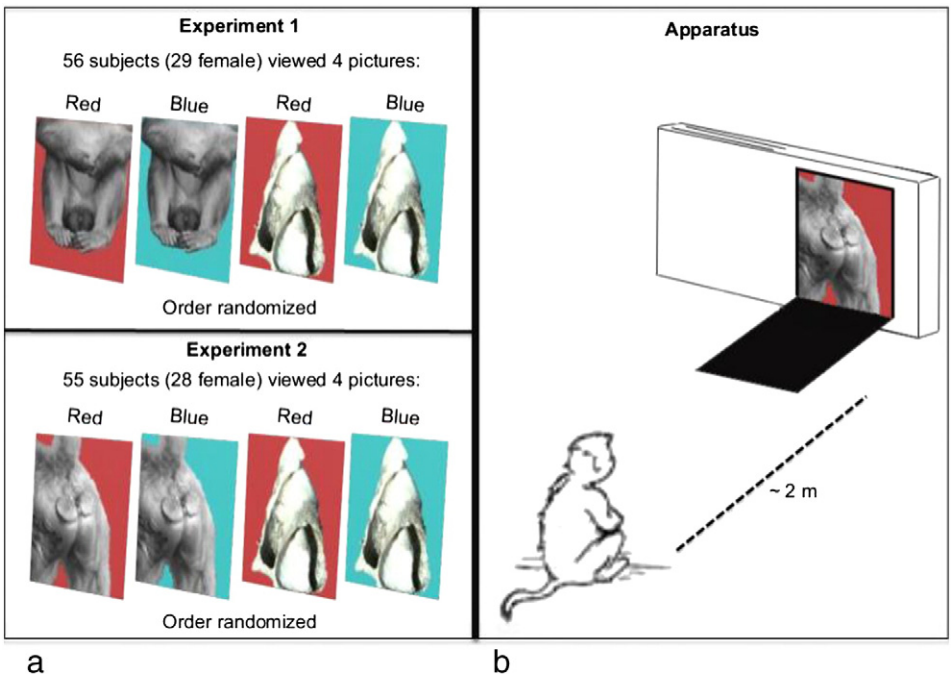

Fig. 1. a: In Experiment 1, male and female rhesus macaques viewed four images in random order: a black and white male scrotum on a red background, a black and white male scrotum on a blue background, a black and white seashell on a red background, and a black and white seashell on a blue background. In Experiment 2, male and female macaques viewed four images in a random order: a black and white female hindquarter image on a red background, a black and white female hindquarter image on a blue background, a black and white seashell image on a red background, and a black and white seashell image on a blue background. b: These images were presented to the subject in a white foamcore box (50 cm long × 5 cm deep × 25 cm tall), with a port through which the image could be displayed. The apparatus was placed ~2 m from the subject.