Animal Behaviour 94 (2014) 61–71

Contents lists available at ScienceDirect

Animal Behaviour

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

Colour and contrast of female faces: attraction of attention and its dependence on male hormone status in *Macaca fuscata*

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ARTICLE INFO

Article history:
Received 19 December 2013
Initial acceptance 16 January 2014
Final acceptance 16 May 2014
Available online 26 June 2014
MS. number: 13-01048R

Keywords:
chromaticity
colour contrast
DKL colour space
faecal steroids
female facial skin
Macaca fuscata
visual preferences

Colour signals play a major role in social and sexual communication in a broad range of animal species. Previous studies on nonhuman primates showed that intense female skin coloration attracts male attention. We investigated (1) whether sexually active male Japanese macaques are attracted by intensely coloured female skin, (2) whether a preference for intense skin coloration results from the increased colour contrast between the skin area and its surroundings irrespective of the red chromaticity, and (3) whether the endocrine status of sexually active males affects their attentional selectivity (or preference) for salient female sexual skin coloration. We conducted two behavioural experiments in two consecutive mating seasons. First, we presented two female face images coloured in a natural range of red skin coloration on monitors. Second, we presented the same faces dissociated from the red chromaticity while maintaining their initial colour contrast properties. In both experiments we analysed male selective visual attention and approaches as a function of stimulus type. Faecal samples were collected after each experiment to analyse focal males' cortisol and testosterone excretion rates. We found that female facial skin coloration triggered selective behaviour in social-living male Japanese macaques. Variances in colour contrast also triggered males' selective orienting towards an intensely coloured face image but the red chromaticity remained essential to induce prolonged male interest. Furthermore, elevated cortisol facilitated male preferences for the intensely coloured female faces, sociosexual stimuli that are presumably highly relevant during the mating season. Future studies may pursue the principle of colour contrast in male attentional behaviour with respect to subtle colour changes expressed by females throughout the reproductive cycle. Cortisol-related physiological processes should be considered in studies on mating-relevant selective attention.

Many animals have a highly adaptive visual system to select behaviourally relevant stimuli within a complex environment. These selective mechanisms are collectively termed selective visual attention and rely on conspicuous visual signals. Colour signals in particular play a major role in social and sexual communication in a broad range of animal species (Bielert, Girolami, & Jowell, 1989; Butcher & Rohwer, 1989; Cook, Vernon, Bateson, & Guilford, 1994; Hagemann, Strauss, & Leißing, 2008; Hill & Barton, 2005; Pryke, Lawes, & Andersson, 2001; Ratcliffe & Boag, 1987; Setchell & Wickings, 2005; Setchell, Wickings, & Knapp, 2006).

In primates, colour signals are fundamental for interindividual communication and may have driven the evolution of trichromatic colour vision (Changizi, Zhang, & Shimojo, 2006). Catarrhine primates, including humans, developed retinal photoreceptors with light absorbance peaks in either shortwave ('blue'), medium-wave ('green') or longwave ('red') spectral bands (Dacey, 2000; De Valois, De Valois, & Mahon, 2000). This trichromatic configuration allows individuals to discriminate between subtle differences in skin reflectance spectra of conspecifics (Changizi et al., 2006). In humans, differences in facial skin coloration influence perceived health and attractiveness of conspecifics (Fink, Grammer, & Thornhill, 2001). Moreover, preferences for reddish skin are linked to mate choice decisions based on the assessment of physiological fitness or females' reproductive state (Re, Whitehead, Xiao, & Perrett, 2011; Stephen, Coetzee, Law Smith, & Perrett, 2009). In several nonhuman primate females, such as macaques, mandrills or

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http://dx.doi.org/10.1016/j.anbehav.2014.05.022
0003-3472/

baboons, sexual skin reddening increases during oestrous (mediated by oestradiol) and decreases during interoestrous (mediated by progesterone) periods (Czaja, Robinson, Eisele, Scheffler, & Goy, 1977; Setchell et al., 2006; Wallner, Aspernig, Millesi, & Machatschke, 2011). Hence, perceptible changes in sexual skin coloration are assumed to represent visual cues to the timing of a female's fertile period (Dixson, 1983, 1998; Dubuc et al., 2009). These findings suggest that visual preferences for intense red skin coloration play a significant role in directing visual attention towards potential mates. Indeed, previous research on rhesus macaques, *Macaca mulatta*, showed that digital images of conspecific faces and hindquarters with increased skin reddening attracted visual attention more than images with paler skin reddening (Gerald, Waitt, Little, & Kaiselburd, 2007; Waitt, Gerald, Little, & Kaiselburd, 2006).

However, perceptual selection of salient skin coloration could rely on a more general principle, namely the enhanced colour contrast between the reddish hairless skin and its surroundings, irrespective of the particular red chromaticity. There is good evidence that feature contrasts, for instance in colour but also other features such as luminance, play an important role in allocating visual attention. This has been demonstrated by single-cell recordings from visual areas of the macaque brain (Arcizet, Koorosh, & Bisley, 2011; Bichot, Rossi, & Desimone, 2005; Constantinidis & Steinmetz, 2005; Thompson & Bichot, 2005) as well as by numerous experimental studies on visual attention in humans (e.g. Bogler, Bode, & Haynes, 2011; Itti & Koch, 2001; Theeuwes, 1992; VanRullen, 2003) and macaques (Higham et al., 2011). Thus, the underlying mechanism for directing attention towards intensely coloured skin regions might rely on high salience caused by enhanced colour contrast between the skin and its surroundings (e.g. fur) rather than the red chromaticity per se. One aim of the present study was to shed light on the role of colour versus colour contrast for male primates' visual and behavioural selection of female faces. In addition, the perception of any sociosexual signal, be it colour or colour contrast, may also depend on the receiver's receptivity for mating situations which is partly determined by the underlying hormone status.

A close link between secreted sex steroids and sexual behaviour is well documented. In particular, testosterone has been reported to affect reproductive behaviour such as sexual motivation, male–male competition and courtship behaviour in several species (e.g. Bagatell, Heiman, Rivier, & Bremner, 1994; Creel, Creel, Mills, & Monfort, 1997; Dixson, 1998; Fusani, 2008; James & Nyby, 2002; Udry, Billy, Morris, Groff, & Raj, 1985; van der Meij, Almela, Buunk, Fawcett, & Salvador, 2011). Recently, the relationship between a perceiver's endocrine status and its interest in socially relevant stimuli has been investigated. The viewing time of threatening stimuli is prolonged by testosterone in macaques and humans (van Honk et al., 1999; Lacreuse et al., 2010; Wirth & Schultheiss, 2007). Similarly, stressed male macaques pay increased attention towards conspecific fight scenes (Bethell, Holmes, MacLarnon, & Semple, 2012). Experiments that measured self-paced viewing times in humans provide evidence for a relationship between elevated testosterone and increased interest in sexual stimuli (Rupp & Wallen, 2007). A further influence on sexual behaviour might be mediated via cortisol, a steroid that regulates energy consumption and retention but also sensory and behavioural alertness in response to stress (Nelson, 2005). These physiological processes are beneficial for efficient mating and competing strategies which come at high metabolic costs, reflected by elevated hormone levels (Bercovitch & Ziegler, 2002). In line with this, cortisol is assumed to facilitate sexual arousal by providing metabolic energy in mating-relevant situations (Goldey & van Anders, 2012). However, an effect of hormones on the allocation of attention to sociosexual stimuli, such as salient sexual skin regions, has not yet been investigated in nonhuman primates. This is surprising, since in seasonally breeding primates, distinctive peaks in male testosterone and cortisol levels are clearly observable during the annual mating season (Barrett, Shimizu, Bardi, Asaba, & Mori, 2002; Nigi, Tiba, Yamamoto, Floescheim, & Ohsawa, 1980).

In light of the aforementioned findings, the present study investigated visual preferences for different skin colour intensities of face images in relation to the endocrine status in male Japanese macaques. The sexually active period of this species is limited to the winter months. In nonlactating females the elevated progesterone and oestrogen levels during the mating season are accompanied by a remarkably intense coloration of the bare face, hindquarter and nipple skin regions (Fujita, Sugiura, Mitsunaga, & Shimizu, 2004; Wallner et al., 2011). Elevated testosterone and cortisol levels of sexually active males are accompanied by increased mating activity and aggressive male–male competition (Barrett et al., 2002; Nigi et al., 1980). We investigated (1) whether sexually active male Japanese macaques are attracted by the intense red coloration of a female face, (2) whether a preference for intensely coloured sexual skin results from the increased colour contrast between the skin area and its surroundings irrespective of the particular red chromaticity, and (3) whether the endocrine status of sexually active males affects their attentional selectivity (or preferences) for salient female sexual skin coloration.

In two consecutive mating seasons we conducted two behavioural experiments in a semifree-ranging troop of Japanese macaques. In our first experiment, males were confronted with two female face images coloured within the natural range of skin reddening found in female Japanese macaques. Given the signalling value ascribed to sexual skin reddening, we predicted that males would express a pronounced preference for the intensely coloured face measurable by increased attention and approaching behaviour. To address the question whether differences in colour contrast of the two presented face images explain attentional preferences, we repeated the initial experiment by using modified versions of the original facial stimuli. The naturally coloured stimuli were transformed to their chromatic opposites, and were thus dissociated from the red chromaticity but conserved in their natural objective differences in colour contrast between the hairless skin and its surroundings. Finally, we hypothesized that elevated testosterone and cortisol levels increased male attentional selectivity for the intensely coloured female faces, sociosexual stimuli that are presumably highly relevant during the mating season. To test this hypothesis we analysed faecal testosterone and cortisol metabolites in relation to males' attentional and behavioural preferences.

METHODS

Observation Site and Animals

Our study took place at the Affenberg Landskron (Affenberg Zoobetriebsgesellschaft mbH), Carinthia, Austria. In 1996 a group of 39 Japanese macaques, *Macaca fuscata*, was brought to the park from Minoo City, Japan. At the beginning of our study in winter 2011 the park housed 126 Japanese macaques (30 adult males, 52 adult females, 35 juveniles and nine offspring) on an area of approximately 4 ha. The vegetation of the park (coniferous and deciduous trees) enables the animals to forage for themselves (e.g. on leaves, herbs, fungi, fallen seeds and insects). Additionally food is provided from the animal care staff of the Affenberg Landskron every day in the morning (1000 hours) and in the afternoon (1500 hours) at a feeding site (i.e. an open area in the middle of the park). This food consists of different kinds of vegetables, fruits and pellets, including trace elements and fibre (in total 120 kg for the whole population). Close to the feeding site a hut, built in 1996, is