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Human colour in mate choice and competition

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Summary

The colour of our skin and clothing affects how others perceive us and how we behave. Human skin colour varies conspicuously with genetic ancestry, but even subtle changes in skin colour due to diet, blood oxygenation, and hormone levels influence social perceptions. In this review we describe the theoretical and empirical frameworks in which human colour is researched. We explore how subtle skin colour differences relate to judgements of health and attractiveness. Also, because humans are one of the few organisms able to manipulate our apparent colour, we review how cosmetics and clothing are implicated in courtship and competition, both inside the laboratory and in the real world. Research on human colour is in its infancy compared with human psychophysics, and colour research in non-human animals, and so we present best-practice guidelines for methods and reporting, which we hope will improve the validity and reproducibility of studies on human colouration.

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Introduction

Unlike most other animals, humans have the ability to use and interpret colour where it does not naturally occur [1] and we imbue colours with complex meanings [2]. Colour can indicate group support or membership [3], represent abstract emotional states (e.g., the 'green-eyed monster' of Shakespeare's Othello that symbolises jealousy), and is involved in cultural rituals and symbolism (e.g., mourning is associated with black in the UK, but with white in India and China, and gold and silver in Taiwan [3]). We know how the eye and brain process colour stimuli [4, 5], how colour terms are represented in language [6], and how colour influences human behaviour in the context of diverse applied fields such as advertising, workplace productivity, and food [7]. In contrast, human colour and its effects on mate choice and competition is an emergent field of research [8].

Individuals vary in colour across their skin, and these differences affect how individuals are perceived [9]. For example, facial skin colour affects perceptions of a person's health and attractiveness [10]. Colour may also be involved in perceptions of emotional state, as suggested by Darwin [11], who described how emotional states might be conveyed by face colour in *The Expression of the Emotions in Man and Animals,* noting that human faces redden or turn deathly pale with rage. Unlike most other animals, humans modify our appearance through various forms of ornamentation, such as cosmetics and clothing. These voluntary signals may have replaced the physiological signals seen in other non-human animals.

In this review, we will evaluate the theoretical and empirical research on human coloration, focussing on the physiological correlates and perceptual influences on attraction, health, and dominance. The first aim of our review is to describe the theoretical and methodological frameworks that underpin this research. The second aim is to review the evidence that facial skin colour is used in judgements of health, that skin and ornamentation colour influence attractiveness and other aspects of mating psychology, and that colour is relevant to dominance and competitive performance. The third aim of our review is to provide guidelines for improving the methods, reporting, and reproducibility of studies on human colour, and to highlight topics for future research.

We note that human skin colour varies with genetic ancestry ([12, 13]) and there are well-documented links between such skin colour variation and how individuals are perceived and treated by others [14]. A review of this literature it outside the scope of the current paper, in which we focus instead on variation in skin colour due to sex, diet, hormones, and other variables, and on coloured ornamentation. Our methodological guidelines are applicable to the study of all forms of human colour differences.

1. Theoretical and methodological frameworks that underpin research on human colour

Theoretical framework

Many of the research questions that interest scientists who study human colour overlap with those investigated in the non-human animal literature [15], and are therefore grounded within the same theoretical framework. For example, in both humans and non-humans, some colour signals are proposed to arise from the evolutionary pressures on females to select healthy, disease-free mates [16], and on males to display their healthy, disease-free state. Both human and non-human signals are studied from a receiver psychology perspective [17]. This theory posits that signals have two distinct components. The first is the 'strategic design' which arises from the selective pressure acting on the content of, or information encoded in, the signal [17]. For example, in humans, facial skin colour is proposed to have evolved to signal health or physical condition [10]. The second aspect of receiver psychology comes from the understanding that many species' signals have arisen for the same function, but the particular signal one species uses is often completely different from the signal another species uses [17]. Therefore, researchers of human and non-human signals also investigate the 'tactical design' or 'efficacy' of signals – this is what makes the signal detectable, easy to discriminate, and/or memorable [17]. For example humans who have redder skin are perceived as more healthy and are judged more attractive by other humans, which is proposed to lead to enhanced signaller fitness. However, unlike may studies in non-human animals, most studies of human colour have not measured, or are unable to measure, true Darwinian fitness.

In addition to receiver psychology, social psychologists Elliot and Maier have developed a model for how colour affects psychological functioning in humans - color-in-context theory (CIC [8]). CIC theory has six core premises. The first is that colour is not only about aesthetics, but also carries meaning and functional value. Second, colours become associated with positive or negative meaning and affect behaviour. For example, colours that carry positive associations evoke approach-oriented psychological processes. Third, responses to colour are automatic (responses occur without conscious awareness). Fourth, responses to colour derive from both innate biological preferences but also from learning. Fifth, colour perception varies as a function of the psychological state of the perceiver. Sixth, and finally, that colour carries different meanings in different contexts.

We don't see the two frameworks as mutually exclusive. Both approaches propose that colour carries meaning, and therefore has a function; both recognise that preferences do not have to be unlearned, but can be acquired through experience and learning; and both frameworks emphasise the advantages of studying the cognitive mechanisms of receivers. However, where the two frameworks differ is that the receiver psychology approach can be directly translated into clear, testable hypotheses, whereas it is more difficult to make precise hypotheses with CIC theory (this has also been recognised by Elliot [18]). We see that using principles from both approaches could be useful in research on human colour, because this would not only allow us to understand the strategic component (the content) of signals*,* but CIC theory could also provide novel ideas about how the signals have their effects. Together, both receiver psychology and CIC theory could provide both ultimate and proximate explanations for human colour. We think that Guilford and Dawkins [17] represent this in the last statement of their paper (p. 10).

"However much we understand the strategic component of signal design, we will never explain why signals are the way they are and why they differ so greatly from species to species until we have a clearer idea of how they have their effects."

Methods used in research on human colour

To assess the different methods used, and parameters reported, in research on human colour, we conducted a Web of Science search for papers published between 2014 and 2016 (October) using the terms color (in no searches did entering 'colour' provide results beyond those provided by 'color') and attractiveness (n=173 results), color and attraction (n=271), color/coloration and health (n=6228 and n=72), color and health and attractiveness (n=25), color and dominance (n=272), color/coloration and competition (n=535 and n=63), color and contests (n=588), and coloration and mate choice (n=161). We excluded review papers, methodological papers, research on clinical or pathological colour measurement, papers that focussed on non-human animals, papers that assessed the colour of products and foods, papers that quantified spatial (i.e., skin topography) rather than chromatic properties of human colour, and papers that focussed on appearance without measuring colour, or that measured colour preferences without quantifying colour. The final set of 16 papers included only those that used either a spectrophotometer (n=2), camera (n=12), or colour chart (n=2) to measure colour (see Supplementary Material).

In comparison to the 60 papers on non-human animal reviewed by White et al. [19], researchers focussing on human colour predominantly use photography (75%), whereas researchers of non-human animal colours are most likely to use a spectrophotometer to measure colour (85%). Photography is fast, allows for distance between the researcher and the participant, and permits analysis of a larger area rather than a limited number of point samples [20]. However, perhaps because photography is more accessible and perceived as a simpler process than spectrophotometry, the application and reporting of this method is often less rigorous (see also [21]). Our literature review revealed that detailed descriptions of photograph acquisition and standardization are often missing, and this may impede analysis of the discrepancies between papers and accurate replication of findings [19, 21]. Most studies reported the camera model (75%). However, camera lens (25%), camera to sitter distance (33%), focal length (17%), and camera settings (25%) were reported less often. Lighting conditions were described in 83% of the papers, although the level of detail varies. A set of guidelines for reporting of parameters would improve the reproducibility of colour measurement research in humans (see Table 1).

Research on animal colour is increasingly employing methods that model signals in the receiver's colour spaces by incorporating the spectral sensitivity and number of retinal photoreceptors in calculations [22, 23]. Research on human colour also models how signals are perceived by the human visual system by calculating the distance between two colours in the International Commission on Illumination (CIE) LAB space (67% of studies in our sample). In this system a difference between colours is described in ΔE units, where ΔE 1 is the smallest difference visible by the human perceptual system (but see [24] which states a ΔE of 2.2). However, recent psychophysical experiments suggest that the human colour perception system is optimized for detecting relatively subtle changes in facial redness, compared with detecting changes in the redness of other types of stimuli or detecting changes in facial coloration on other colour axes [25]. Discrimination thresholds for within-subject changes in facial redness are very low (e.g., ΔE 0.67 [26]), and when asked to discriminate between the healthiness and attractiveness of faces differing in carotenoid colour (see section two), participants are sensitive to differences of ΔE 1.37 and ΔE 1.55, respectively. There is a clear discrepancy in what value of ΔE constitutes a discriminable difference in the context of human skin colour. ΔE may be as low as 0.67 [26] or as high as 2.2 [24]. This topic warrants further study

Where colour has not been modelled in CIE LAB, researchers have analysed RGB values alone [27]. This is a more convenient method because most consumer cameras output images as JPGs, with each pixel assigned a red, green, and blue value. However, the use of uncalibrated RGB values do not represent colour as it is processed by the human visual system, because cameras respond nonlinearly to light intensity and are biased towards certain wavebands, particularly the long (red) [28]. Researchers who neither report correcting for these problems, nor state how the changes in colour they describe would be perceived by humans, could have identified effects that are inaccurate or, if genuine, so small as to be biologically irrelevant [29]. Only 50% of the studies we reviewed reported the colour standards used to standardise colour, and only 33% controlled for the camera's nonlinear responses to changes in light intensity and/or radiance [28]. These details are essential for assessing the validity of colour metrics.

Most (but not all) of the studies on human colour to date have been conducted in Western countries on White participants (mainly university students). Therefore, although statements of universal colour preference pervade the literature [30], readers of this review should keep in mind that there is not solid support for certain colour traits as cross-cultural indicators of good health, fertility, or dominance [31].

2. Empirical findings on human colour

Research on Colour in Health and Attractiveness

Perceptions of a person's health and attractiveness are based partly on characteristics of face shape, such as symmetry and masculinity/femininity [32]. Although face shape may reflect a person's physical and mental health [33-35], better estimates of current or recent health may be based on more labile cues, including facial skin colour [10].

Skin colour: blood oxygenation and carotenoids

When researchers give participants the ability to manipulate the overall colour of facial images to optimise apparent healthiness, they increase redness (the *a** axis of the CIE LAB human colour space; Commission Internationale d'Eclairage), yellowness (*b**), and lightness (*L**) [36]. Further studies have indicated that yellower and redder skin is also more attractive in male faces [37, 38].

Skin yellowness and redness are probably linked to health and attractiveness because these colour properties vary with current health [39]. Regarding long-term physical condition, blood perfusion and oxygenation, which are reduced when a person's health or cardiovascular fitness is poor, are linked to reduced skin redness [40, 41]. When asked to adjust the colour of male and female facial images to optimise their healthy and attractive appearance, participants increase skin blood colour [26, 42]. When judging for health and attractiveness, participants discriminate between faces differing in oxygenated blood colour at similar ΔE thresholds [26]. This suggests that perceptions of attractiveness and health that are based on skin redness might be closely linked. There is also evidence that facial healthiness mediates the effect of red skin colour on female sexual attractiveness [43].

Focussing on current health, human participants who are injected with a bacterial endotoxin to induce acute sickness exhibit noticeable changes in their skin after only one hour—facial skin becomes lighter and less red, while arm skin becomes darker, less red, and less yellow. Colour changes peak when participants' subjective ratings of illness are at their highest [39].

Skin yellowness and darkness are driven by melanin and carotenoid pigments [44, 45]. These pigments are related to health: among other benefits, carotenoid supplements increase T-lymphocyte numbers [46], and melanin protects against ultraviolet radiation damage to DNA [47]. When participants are tasked with optimising the healthy appearance of faces, they adjust skin colour to increase carotenoid and melanin colouration, but favour differences based on carotenoids [48]. Skin tanning, in which exposure to the sun stimulates melanisation of the skin, is attractive in Western countries like the UK [49]. However, carotenoid colouration increases attractiveness more than melanin colouration, and this effect is stronger for female than male faces [50]. Consuming approximately three extra portions of carotenoid-rich fruits and/or vegetables per day is enough to induce a change in skin colour that increases perceptions of health and attractiveness [51].

These facial skin colour preferences are unlikely to be explained by sensory biases or preferences for particular colours. Detection thresholds for changes in carotenoid and blood oxygenation colouration are lower than thresholds for healthiness and attractiveness [26, 51], whereas we would expect identical thresholds if social perceptions were based solely on detectable colour differences. Furthermore, the attractiveness of non-face stimuli is not influenced by carotenoid colouration [52]. From a receiver psychology perspective, increases in skin redness and yellowness are detectable and discriminable, and make an effective signal of current as well as long term health (this is the strategic design of a health signal within a receiver psychology framework)

Skin colour distribution

In most studies of face colour, photographic stimuli are manipulated such that all areas of facial skin are altered uniformly. These manipulations may not represent how colour varies naturally. Differences in colour homogeneity, due to melanin and haemoglobin distribution patterns, vary with age [53]. The relative luminance or hue of features such as the eyes and the lips and the surrounding skin also influences how faces are perceived: the faces of middle-aged women rated as healthy in appearance tend to have more luminous periorbital regions and sclerae (the whites of the eyes) and redder cheeks and lips [54]. The luminance of the eyebrows, eyes, and mouth is lower than that of the surrounding skin in younger women [55], and decreasing the luminance of the features and increasing that of overall facial skin makes female faces more attractive and male faces less attractive [56]. Female faces exhibit greater facial contrast at the eyes and mouth than do male faces, to the extent that varying the contrast of an androgynous face while keeping the shape of the face constant can induce the viewer to perceive the face as male or female [57]. However, most studies on contrast have used greyscale stimuli, which suggests the possibility that viewers are attributing changes in luminance to changes in other colour channels.

Colour and human ornamentation

Unlike other animals, humans are able to modify our appearance through various forms of ornamentation, such as cosmetics and clothing. Most work on this topic has centred on women’s use of the colour red to enhance their attractiveness.

Use of cosmetics

Empirical research on makeup use and face colour is in its infancy: authors have generally been interested in natural differences in face colour, and request participants remove any makeup before being photographed. Russell [58] photographed women both with and without self-applied makeup and reported that the contemporary “received style” of makeup among women in industrialised nations is typified by lips darkened and reddened with lipstick, cheeks reddened with blusher, periorbital regions darkened with eye shadow and mascara, and the overall colour of facial skin rendered more homogeneous with foundation. This style may be popular because it emphasises the colour patterns that differentiate women from men and young from old [59]. Make-up applied in the received style is attractive to men and influences real-world male behaviour [60-62], as well as enhancing perceptions of women's health, confidence, and earning potential [63]. We note that cosmetic use is highly subject to fashion and that wearers may adopt non-received styles of makeup for various reasons, such as group identification.

Colour of clothing

The effects of clothing colour on how a person is perceived, and particularly the effects of red clothing on female attractiveness, has received a lot of research interest. Men find women pictured in red (rather than blue) clothing to be more attractive (though see [64]), and express a greater willingness to date a woman in red [65]. The red effect persists outside of the laboratory, with female hitchhikers who wear red more likely to receive an offer of a ride from male, but not female, drivers [66]. Women appear to be aware that red clothing enhances their attractiveness to men. Women interested in casual sex choose to wear red clothing in photographs posted to internet dating websites [67] (men preferentially initiate contact with women who wear red in profile pictures [68]), and prefer red clothing and other forms of ornamentation when expecting to interact with attractive men, while avoiding red ornamentation if an anticipated interaction partner is unattractive [69]. Women perceive other women who wear red (rather than white) as more sexually receptive, and as less faithful to their partners [70]. Women express a greater desire to guard their partner against the advances of a rival wearing red (rather than green) [70], and men are more willing to guard a female partner wearing red (rather than black) [71]. It will be noted that most authors contrast perceptions of red ornamentation with those of a single other colour, and the variety of colours can make it difficult to compare results across studies (but see e.g. [66, 72]).

Although the effects of red ornamentation on the attractiveness of men has received less study, men are perceived to be more attractive when wearing red clothes, an effect that is mediated by perceptions of status [73]. A man's necktie colour may also influence perceived ability in job interviews [74], although it does not affect the perceived competence of politicians [75].

Extended colour stimuli

Colour does not only have an influence on attraction when displayed directly on the skin, but also when seen in close proximity to a person. Women whose photographs are displayed with a border of red, compared to other colours, are rated as more attractive and as higher in sexual desire and sexual intentions [65, 76]. Red does not lead men to view women more positively in general, as it has no effect on ratings of likeability, perceived kindness, or perceived intelligence. A red background has more pronounced effects on attractiveness when the woman pictured is rated at baseline as highly attractive [77], or if she is in her twenties rather than her fifties [78]. There is tentative evidence that this effect may generalise to other cultures [76]. Burkinabé men (a group in Burkina Faso for which red generally carries a negative meaning, such as death, sickness, or bad luck) rate photographs of woman with red borders more attractive than women bordered by blue. The men also report more interest in meeting and courting the woman in the red-bordered photograph.

Colour and the ovulatory cycle

The females of several primate species advertise their ovulatory status through anogenital swelling [79-81], and facial or perineal skin colour may also vary cyclically [29, 82-84]. Although human ovulation is not advertised, as it is in several primate species, there have been reports of women's skin darkening during the luteal (low fertility) phase of the menstrual cycle and during pregnancy ([85] and references within). However, much of this early evidence came from women's self-reports of facial skin change, and participants were often aware of the studies' aims and hypotheses. Furthermore, these studies often lacked objective quantitative colour metrics [86].

There is increasing evidence that women's faces are rated more attractive during the most fertile phase of their menstrual cycle [87, 88]. Cycle effects on facial attractiveness may be underpinned by changes in facial shape [27, 89, 90]. However, because oestrogen and progesterone levels vary over the menstrual cycle [91], and since oestrogen is associated with many aspects of skin physiology, including aging, healing, hydration, hair growth, sebum production, and pigmentation [92-94], recent research has also focussed on hormone-related variation in skin colour.

Early research on hormonal correlates of face colour aimed at revealing differences between women (references within van den Berghe and Frost [85]). We first review that literature before describing more recent research on within-individual differences.

Inter-individual variation in hormones and coloration in women

Oestrogen and progesterone levels vary between women, and those with especially high oestrogen levels during the late follicular (fertile) phase of their cycle are rated as more attractive, feminine, and healthy [95, 96]. These increased ratings of attractiveness emerge only when women are instructed to remove makeup before being photographed [87, 88, 95, 97], which suggests that natural changes in the skin explain these differences.

Higher oestrogen is associated with greater vascularization and blood vessel dilation [98, 99]. Human participants who have had their ovaries removed show changes in the vascularity and luminance of their skin (measured as percentage reflectance with a spectrophotometer) compared to the skin of regularly cycling women [100].

Intra-individual variation in hormones and coloration in women

The evidence for skin colour change across an individual ovulatory cycle is equivocal. Edwards and Duntley [100] were among the first authors to conduct a within-participants longitudinal study on skin colour changes across the cycle. They reported reduced vascularisation during menses, and increased haemoglobin and vascularity after mid-cycle, which could affect perceptions of skin colour (redness) and luminance, but did not model this in human colour space. Samson et al. [97], compared the skin in late follicular (high fertility) and mid luteal phases of women's cycles in CIE LAB and found no effect of fertility status on any of the three colour dimensions, leading the authors to conclude that "differences in men's perceptions of attractiveness and healthiness [are] not driven by these [colour] measures". In contrast, Oberzaucher et al. [27] took photographs of women near ovulation and during the luteal phase, and extracted mean RGB colour values from cheek patches. While they found that skin was redder at periovulation than during the luteal phase, these results should be interpreted with some caution (see section one on methods).

Recently, in a longitudinal study, Jones et al. [101] showed that women's facial skin was significantly redder, but not yellower or lighter, when salivary oestradiol was increased during the cycle. Jones et al. [101] suggest that these colour changes may be detectable by the human visual system, given that discrimination thresholds for within-participant changes in facial redness are lower than for non-face stimuli [26]. However, in a similar longitudinal study, Burriss et al. [20] found that redness was slightly heightened between ovulation and menses, with an average amplitude change of about 0.6 ΔE. This difference is unlikely to be perceivable by the human visual system based on the ΔE range where differences become perceivable [24]. However, a blood perfusion change of 0.67 ΔE is detectable [26]. It therefore remains possible that cyclical changes in skin redness are detectable under perfect laboratory conditions.

Elliot and Niesta [65] speculated that women might augment any cyclical changes in skin colour by adopting red ornamentation near ovulation. Women do appear to wear more red and pink clothing when most fertile [102], especially when the weather is inclement and wearing revealing clothing (another style that women may adopt to attract partners [103]) is a less appealing option [104].

Colour in dominance and competitive performance

Colour and its effects on aggression and dominance

Non-human animals often signal dominance to potential opponents through colourful displays, especially during competitive encounters [105-107]. Many animals also plastically change their colour, for example becoming redder during agonistic encounters (e.g., male turkeys swell their caruncles and become redder) or with changes in dominance (e.g., male mandrills exhibit an increase in testosterone and become redder if a dominance status challenge is successful [108]). However, changes in facial temperature with anger are not always observed in humans [109], nor is it customary to directly measure facial temperature (e.g., forehead pulse amplitude is used as a proxy of facial flushing [110, 111]). To our knowledge, no laboratory studies have attempted to investigate the effects of agonistic interactions on measured human facial colour.

It has also been suggested that human male facial skin redness is also androgen-dependent [37, 112], but this link is based on research that does not quantitatively measure skin colour as it would be perceived by the human visual system [113]. Increasing the redness of male human facial images enhances women's perceptions of dominance and aggression [37], but whether actual dominance/aggression is associated with testosterone and skin colour remains untested.

Colour and competitive sporting performance

The influence of colour on sporting performance has received the most attention from researchers of human colour, both conceptually and empirically. The most colourful animal displays often elicit avoidance or withdrawal behaviour in conspecifics [105, 114] and heterospecifics [115]. These "badges of dominance" can therefore help individuals to assess the competitive ability of their opponent and avoid the costs of escalated aggressive encounters [116]. It is not only naturally conspicuous stimuli that have this effect; animals whose colour signals are augmented by experimenters are more likely to win contests [117, 118]. It is plausible that humans, who are able to manipulate our apparent colour, have augmented physiological dominance signals with voluntary signalling. In support of this idea, it has been demonstrated that testosterone levels are associated with an active choice of red clothing for competitive events [119] (but see [120]), and that individuals who choose red tend to rate their colour as more dominant and aggressive than do those who choose blue [119]. Heart rate is elevated in fighters assigned to wear red compared to those assigned to wear blue, before, during, and after physical combat [121].

Hill and Barton [122] examined the outcomes of the 2004 Olympic combat sports of western boxing, taekwondo, Graeco-Roman wrestling, and freestyle wrestling. In these sports the participants are randomly assigned either red or blue apparel; those fighting in red won more fights and more rounds across all weight classes (though see [123, 124]). Hill and Barton [122] found no significant effects of clothing colour in female combat sports (see also [125]), which may reflect inherent differences in intrasexual competition between the sexes [126].

In non-combat sports such as association football (soccer), red still seems to have an effect (though see [127]). Hill and Barton [122] found that teams wearing red in the 2004 UEFA (The Union of European Football Associations) European Championships scored more goals than when they played in their alternative colours. In the English Football League between 1945 and 2006 the median league position and the mean percentage of maximum possible points were greatest for teams that wore red [128]. Viewing red (rather than blue or green) on a goalkeeper's uniform undermines penalty kick performance [129], and goalkeepers perceive a higher likelihood of saving penalties kicked by players wearing white uniforms rather than red [130].

Viewing red rather than green or blue stimuli has a greater distracting effect for men [131], and red has a negative effect on motor performance of opponents [121, 132]. Red arouses more than blue, and the emotional valence of red may differ for men and women [133]. In non-physical contexts, participants who are presented with the colour red in an achievement context (e.g., an IQ test) preferentially choose easier tasks [134], decrease their walking speed [135], and even physically move away from red stimuli [136] .

It could be that the colour red has less to do with intrasexual competition than with how competitors are perceived by others, a possibility supported by research showing that, independent of the increases in the wearer's own dominance and aggressiveness, wearing red affects the reactions of sports referees [137]. Hagemann et al. [138], using video compositing software, reversed the colour of the head guards and torso protectors worn by taekwondo fighters, and found that judges who viewed the videos awarded significantly more points to a competitor in red than blue, even though the content of the fight was identical across conditions. Krenn [139] digitally manipulated the colour of soccer kits and found that professional referees judged tackles committed by a player wearing red rather than blue as more harsh. Likewise, in the National Hockey League (NHL) and the National Football League (NFL), teams that wore black uniforms were penalised significantly more than teams in other coloured uniforms. This apparent bias in referees' judgements persisted when teams switched from non-black to black uniforms: those that switched to black were penalised more than those that switched to non-black [140]. Therefore, in a competitive context, red is an effective signal because it has effects on both the wearer (signaller) and receivers (opponent and referees) – this is the tactical design in receiver psychology.

3. Broad conclusions

Suggested improvements for methods and reporting of methods

Methods – creating stimuli

It is common practise to present participants with images of a person whose facial skin colour or clothing colour is manipulated using computer graphics software [65, 68, 74, 75, 135, 141, 142]. This method allows the researcher to limit the influence of confounding variables, but a disadvantage is that the manipulation is often unrealistic. For example, clothing colour saturation or luminance levels are sometimes outside the range one might expect to see under normal conditions of lighting and with standard textiles. Furthermore, the colours of facial stimuli are sometimes unrealistic, embodying colours that are not biologically possible. Although this allows researchers to define what makes an effective signal (the tactical design in receiver psychology), it does not allow researchers to conclude that humans are actually using these signals for the strategic purpose of increasing attractiveness, and that these signals are detectable and discriminable. We encourage researchers to create stimuli based on colour manipulations that vary in ecologically relevant and specific units of discriminability (see for example [48, 51, 143]). Researchers should also control for potential wearer effects, whereby the wearer adopts subtly different facial expressions depending on their clothing colour [72], perhaps because they are aware that some types of clothing make them appear more attractive [144]. It is also plausible that any wearer effects are augmented by light reflecting off clothes and casting a noticeable tint on skin tones (colour spill), such that the skin of a person wearing red clothes would appear to be redder and therefore more attractive.

Reporting of methodological parameters

From our survey of papers published on human colour (section one), we have compiled a list of standardisation procedures that are widely utilised by animal colour and basic colour scientists. We list these procedures in Table 1 in order that future research provides detailed descriptions of photograph acquisition and standardization. Our objective is to assist researchers to investigate discrepancies between research results, and allow accurate replication of research [19, 21]. Following these guidelines for reporting of parameters will improve the reproducibility of colour measurement research in humans. We refer readers to White et al. [19] for comprehensive information on spectrophotometry.

4. Concluding remarks

Clearly, overall changes in facial colour and contrast are sufficient to alter face perceptions but do not tell the whole story. For example, while we know that red lips are more attractive, we do not know if this is because they are red or because they are redder than the surrounding skin, or whether dark periorbital regions appear less healthy because they are dark or because they are darker than the surrounding skin. Studies in which the colour of facial skin outside of specific features or regions is manipulated independently, and to the same degree, as the colour of facial skin within these features and regions will allow researchers to test whether any effects of contrast are independent of those attributable to overall colour.

Given the connections between red and aggression and dominance, as well as the suggestion by Changizi et al. [145] that colour vision in primates was selected for discriminating emotional states, socio-sexual signals, and threat displays (the strategic design in receiver psychology), future research should focus on the tactical design of these potential signals, and investigate the effect of agonistic interactions on human facial colour – whether actual dominance/aggression in men is associated with testosterone and skin colour and that these colour differences are detectable, discriminable, and memorable to receivers. To our knowledge, no one has yet examined how female colour relates to testosterone.

Information to be reported	Reason	Further discussion
Camera model	Camera models differ in spectral sensitivity and responses to changes in light intensity and/or radiance.	Stevens *et al.* [22, 28]
Camera lens	Optics can introduce spherical and chromatic aberration.	Remondino & Fraser [146]
Camera to sitter distance	The distance of the sitter's face to the film/sensor plane of the camera can affect how faces are perceived. A distance of 2m was most frequently preferred in one study.	Bryan *et al.* [147]; Verhoff *et al.* [148].
Focal length	Often confused with camera to sitter distance, focal length is the distance between the lens and the image sensor. Wider angle lenses (short focal length e.g. 10-28mm) make a face appear to bulge towards the camera, enlarging the nose relative to the ears, while telephoto lenses (long focal length e.g. 100mm +) make a face appear "flatter". A constant focal length of 40-60mm is advised.	Banks *et al.* [149]; Třebický *et al.* [21]
Camera settings (F-stop, shutter speed, ISO, white balance)	Exposure, aperture, and white balancing varies across cameras and will often produce data in which outputs (e.g. RGB values) are incorrectly weighted.	White *et al.* [19]
Lighting conditions	Colour perception is not only a function of lightness, chroma, and hue, but also the amount and type of ambient light. Cross polarized filters may be used to capture skin colour information that is not influenced by shadows or highlights.	Fink *et al.* [150]
Background colour/sitter's clothing	Clothing colours, especially near to the area being photographed, may cast a noticeable tint on skin tones (colour spill), or affect the colour saturation and brightness of the photo. Given the evidence that women's choice of clothing is confounded with variables of interest, standard clothing should be used to limit the effects of clothing on appearance.	Lindner & Winkler [151]; Burriss *et al.* [152]
Colour standards	Colour standards are necessary to correct for both ambient light and camera biases toward specific wavelengths. Each pixel value should be the same in each colour channel with respect to a grey standard.	Stevens *et al.* [28]
Sex of the photographer	The sex of the photographer can influence the sitter's facial temperature. If increases in temperature are associated with blushing, the sex of the photographer may also affect the sitter's skin colour.	Hahn *et al.* [153]
Time of year	Differences in sun exposure can affect skin colour measurements.	Jablonski & Chaplin [12]
Image format	Compressed file formats (e.g. JPEG) may introduce chromatic and spatial artefacts to images, whereas uncompressed formats (i.e. TIFF and RAW) typically do not. If compressed files are used, or if files are compressed during processing, the level of compression should be reported.	Troscianko & Stevens [23]
Software for image processing	A range of available software programs can be used to analyse and to calibrate the content of digital images, including MATLAB (The Mathworks Inc. Natick, MA), Image J, and Adobe Photoshop (Adobe Systems Inc., San Jose, CA).	Stevens, Stoddard & Higham [22]
Linearization of sensor outputs	Cameras respond nonlinearly to changes in light intensity and/or radiance, and are biased towards certain wavebands, particularly the long (red), meaning that data from nonlinear images will almost always under- or overestimate true object values. A linear response to radiance is essential if one is to convert images to visual system spaces. Given the possibility of eye-camera metamerism, 40 to 60 colour samples is recommended for using colour charts.	Stevens et al. [28]; Stevens, Stoddard & Higham [22]

Future research that replicates in non-White participants the effects seen in studies with White participants may reveal whether skin colour judgments of health and attractiveness are universal, as are preferences for facial symmetry [154]. For example, oestradiol levels are higher at all points of the cycle in African American compared to White American women [155]; as oestrogen is implicated in cyclic variation in phenotype [88, 101, 156-158], facial attractiveness may vary differently in women of different ethnicities. Cross cultural research on judgements of health would be worthwhile: one study has shown that Black African observers tend to rely more on skin colour when judging the attractiveness of in-group faces, while White Europeans tend to rely more on face shape [159]. This research would lend support to the strategic design of facial colour – that it signals qualities that are attractive to potential mates or enhance intrasexual competitiveness, and may have evolved through sexual selection to enhance reproductive success (the strategic design). This may also provide important evidence for the evolutionary origins of these potential signals in humans.

5. Author contributions

Both authors equally contributed to the conception of the review. HMR collected the data. Both authors interpreted the data and conceived the recommendations. Both authors equally contributed to writing the article.

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