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Social Perception of Facial Color Appearance for Human Trichromatic Versus Dichromatic Color Vision

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Abstract

Typical human color vision is trichromatic, on the basis that we have three distinct classes of photoreceptors. A recent evolutionary account posits that trichromacy facilitates detecting subtle skin color changes to better distinguish important social states related to proceptivity, health, and emotion in others. Across two experiments, we manipulated the facial color appearance of images consistent with a skin blood perfusion response and asked participants to evaluate the perceived attractiveness, health, and anger of the face (trichromatic condition). We additionally simulated what these faces would look like for three dichromatic conditions (protanopia, deuteranopia, tritanopia). The results demonstrated that flushed (relative to baseline) faces were perceived as more attractive, healthy, and angry in the trichromatic and tritanopia conditions, but not in the protanopia and deuteranopia conditions. The results provide empirical support for the social perception account of trichromatic color vision evolution and lead to systematic predictions of social perception based on ecological social perception theory.

Keywords

trichromatic, color vision, social perception, evolution, face color

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The human face is a wellspring of social information; we can make rapid judgments about a wide range of social characteristics (e.g., sex, race, age, attractiveness, health, emotion) based on only a brief exposure to facial stimuli (Weisbuch & Ambady, 2011). Although a majority of traditional social psychological research has focused on assessing how these judgments influence downstream phenomena (e.g., stereotyping and behavior), only recently have researchers focused on elucidating the lower level perceptual mechanisms that produce these judgments in the first place (Freeman & Ambady, 2011; Oosterhof & Todorov, 2008). An emerging line of research has demonstrated that one such perceptual mechanism that can independently influence a range of social judgments is facial color appearance (for reviews, see (Rowland & Burriss, 2017; Stephen & Perrett, 2015; Thorstenson, 2018). This work suggests that human color vision plays a key role in social perception processes. In the current article, we briefly review theoretical accounts of human color vision evolution, including a recent account driven by *social* evolutionary considerations. We then overview the existing literature on the role of facial color appearance in the expression and perception of social characteristics (i.e., attractiveness, health, and emotion), grounded in an ecological theory of social perception (Zebrowitz-McArthur & Baron, 1983). Finally, we report two experiments that provide an empirical test of the social evolutionary account of human color vision.

Typical human (and most primate species) color vision is considered trichromatic, meaning we possess three distinct classes of wavelength-sensitive photoreceptive cells called cone photorecepters, or cones, that allow us to discriminate chromatic colors across the visible spectrum. These cones are distinguished as short wavelength (S; with peak sensitivity at ~430 nm), medium wavelength (M; with peak sensitivity at ~535 nm), and long wavelength (L; with peak sensitivity at ~562 nm; Jacobs & Deegan, 1999). Whereas most mammalian species possess dichromacy (having one S cone and one M/L cone), trichromacy in humans and most nonhuman primate species evolved when the older M/L cone opsin gene duplicated and diverged into two separate M and L cones (Dulai, von Dornum, Mollon, & Hunt, 1999).

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The functional significance of trichromacy evolution is currently under debate. A popular account suggests that trichromacy was selected to aid primates in foraging by facilitating the detection of ripe fruit against green leaves (Allen, 1879; Lucas et al., 2003; Mollon, 1989; Osorio & Vorobyev, 1996; Surridge & Mundy, 2002). While there is support demonstrated for this hypothesis (Bunce, Isbell, Grote, & Jacobs, 2011; Caine & Mundy, 2000; Melin et al., 2009; Osorio, Smith, Vorobyev, & Buchanan-Smith, 2004; Regan et al., 2001; Smith, Buchanan-Smith, Surridge, & Mundy, 2003; Smith, Buchanan-Smith, Surridge, Osorio, & Mundy, 2003; Sumner & Mollon, 2000; Vorobyev, 2004), some ecological studies do not observe a benefit of trichromacy on foraging behavior (Hiramatsu et al., 2008; Vogel, Neitz, & Dominy, 2007). Other theoretical accounts of color vision variation in primates that have received less empirical attention include camouflage detection, predation detection, and nocturnal versus diurnal activity (see Kawamura & Melin, 2017, for a comprehensive review).

Alternatively, a more recent functional account posits that trichromacy may have been selected by *social* evolutionary pressures (Changizi, 2010; Changizi & Shimojo, 2011; Changizi, Zhang, & Shimojo, 2006). Specifically, this account suggests that the divergence of M and L cones allows for the optimal detection of socially relevant skin color appearance fluctuations in others. Changizi and colleagues (2006) note that changes in dermal hemoglobin oxygenation and concentration lead to predictable changes in the spectral reflectance (and consequently visible color) of skin. Increases in hemoglobin oxygenation heighten relative L-cone to M-cone activation, resulting in redder skin appearance (while decreases in hemoglobin oxygenation produce the opposite, resulting in greener skin appearance). Increases in hemoglobin concentration tend to increase M- and L-cone activation relative to the S cone, resulting in blue skin appearance, whereas decreases in hemoglobin concentration produce the opposite, resulting in yellow skin appearance (see also Thorstenson, 2018 for a review). Importantly, Changizi and colleagues (2006) demonstrated that M- and L-cone sensitivities in trichromats are situated in the visible spectrum such that they are able to optimally detect these skin color appearance fluctuations. This correspondence, between the spectral sensitivity of trichromatic photoreceptors and spectral fluctuations of skin enduring transient hemoglobin changes, presumably enables particular sensitivity to discriminate socially relevant physiological conditions (e.g., emotional states, sexual signals, and threat displays). It has also been noted that trichromatic primates tend to be bare-faced, allowing rapid access to visual skin color appearance modulations. See Figure 1 for an illustration of the spectral characteristics of human skin and trichromatic photoreceptors. While there is some recent work supporting this hypothesis for viewing nonhuman primate targets (Hiramatsu, Melin, Allen, Dubuc, & Higham, 2017) research in this area is still sparse and has yet to be conducted using human targets.

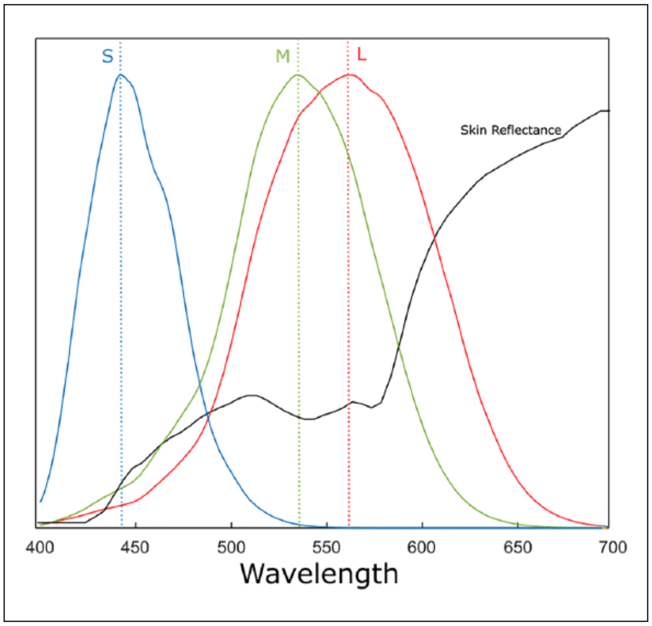

Figure 1. Spectral sensitivities of the S (blue), M (green), and L (red) photoreceptors and the spectral reflectance of typical human skin along the visible spectrum.

Note. Dotted lines are placed at peak cone sensitivities. Modulations of blood flow mostly affect the "W" feature (~525-575 nm) of skin reflectance, influencing changes in skin color appearance (Changizi, Zhang, & Shimojo, 2006).

An ecological theory of social perception holds that social perception processes serve an adaptive function (Zebrowitz, Bronstad, & Montepare, 2011; Zebrowitz-McArthur & Baron, 1983). Perception facilitates goal attainment and species propagation by informing behavior (Gibson, 1979). This ecological approach to social perception assumes that (a) the external environment provides information to guide biologically and socially functional behaviors, and (b) the successful transfer of this information relies on a compatibility between a signal (stimulus information) and the perceiver (perceptual system). In the current investigation, we focus on the stimulus information (facial color expression) and the perceptual system (facial color perception) involved in social processes related to evaluation of attractiveness, health, and emotion. We chose to focus on these evaluations because they represent interpersonally important perceptions that shape social interaction and decision making. For instance, perceptions of attractiveness and health guide mating decisions because they provide an indicator of overall mate quality and reproductive potential (Etcoff, 1999; Perrett, 2010; Rhodes et al., 2007; Weeden & Sabini, 2005). Similarly, perceptions of emotion (e.g., anger) inform situational context (e.g., dominance, hostility) and guide behavior (e.g., avoidance; Marsh, Adams, & Kleck, 2005).

Indeed there is evidence that skin color appearance subtly undergoes change as an inevitable consequence of socially relevant states. In nonhuman primates, female skin color appearance becomes redder throughout the ovulatory cycle, when sexual cues afford the most significant reproductive consequences (Bielert, Girolami, & Jowell, 1989; Deschner, Heistermann, Hodges, & Boesch, 2004; Dixson, 1983; Gerald, 2003; Setchell & Wickings, 2004; Setchell, Wickings, & Knapp, 2006; Waitt, Gerald, Little, & Kraiselburd, 2006). Skin color appearance in male nonhuman primates also influences female preferences by signaling elevated testosterone (Rhodes et al., 1997; Waitt et al., 2003). In addition, there is evidence that the same skin color appearance modulations occur in human females (Burriss et al., 2015; Edwards & Duntley, 1949; B. C. Jones et al., 2015; McGuiness, 1961; Oberzaucher et al., 2012; Snell & Turner, 1966; van den Berghe & Frost, 1986) and possibly males (due to elevated testosterone; Miller & Maner, 2010). Furthermore, skin color appearance undergoes change as a consequence of physiological states related to health, including skin vascularization (Changizi & Shimojo, 2011; Charkoudian, 2003; Henderson et al., 2017; Panza, Quyyumi, Brush, & Epstein, 1990; Ponsonby, Dwyer, & Couper, 1997; Sibenge & Gawkrodger, 1992; Wilkin, 1994), bilirubin (Knudsen & Brodersen, 1989), melanin (Stamatas, Zmudzka, Kollias, & Beer, 2004; Zonios, Bykowski, & Kollias, 2001) and carotenoids (Alaluf, Heinrich, Stahl, Tronnier, & Wiseman, 2002; Coetzee & Perrett, 2014; Tan, Graf, Mitra, & Stephen, 2015, 2017; Whitehead, Re, Xiao, Ozakinci, & Perrett, 2012). Finally, there is a sizable literature examining the physiological correlates of experiencing various emotion states, which can then be used to predict how skin color appearance likely changes with respect to these emotions (see Thorstenson, 2018; Thorstenson, Elliot, Pazda, Perrett, & Xiao, 2018, for reviews).

In accord with the above literature showing the relation between socially relevant states and skin color appearance fluctuations, recent research has demonstrated that facial color appearance can independently influence an array of social evaluations related to these states. For instance, facial color appearance can influence perceptions of attractiveness (Carrito et al., 2016; Lefevre, Ewbank, Calder a, Hagen, & Von Perrett, 2013; Pazda, Thorstenson, Elliot, & Perrett, 2016; Re, Whitehead, Xiao, & Perrett, 2011; Said & Todorov, 2011; Stephen, Oldham, Perrett, & Barton, 2012; Thorstenson, Pazda, Elliot, & Perrett, 2016; Young, 2015), health (A. L. Jones, Porcheron, Sweda, Morizot, & Russell, 2016; Re et al., 2011; Stephen, Coetzee, Law Smith, & Perrett, 2009; Stephen, Law Smith, Stirrat, & Perrett, 2009; Young, Thorstenson, & Pazda, 2016), and emotion (Benitez-Quiroz, Srinivasan, & Martinez, 2018; Thorstenson, Elliot, et al., 2018; Thorstenson, Pazda, Young, & Elliot, 2018). Notably, and most relevant to the current work, slightly redder and yellower faces are consistently positively associated with perceived attractiveness, health, and anger (for moderators of this pattern, see also Fisher, Hahn, Debruine, & Jones, 2014; Han et al., 2018; Kandrik et al., 2017).

Considering the social significance of facial color perception, and the hypothesis that trichromatic color vision was selected by social evolutionary pressures to detect socially relevant states in others, it follows that trichromatic color vision should provide an advantage relative to dichromatic color vision in social perceptions arising from differences in facial color appearance. Hiramatsu and colleagues (2017) provided initial evidence of this hypothesis. The researchers presented human observers with pairs of rhesus macaque photographs—proceptive versus nonproceptive faces—and asked them to select the proceptive face. In addition, the researchers presented images that simulated what these face pairs would look like to trichromats (equivalent to the original images) and dichromats (protanopia, deuteranopia, tritanopia), by computationally modeling the visual response from the corresponding cone sensitivities. The researchers found support that the trichromatic image representations conferred an advantage relative to the dichromatic image representations in detecting the proceptive faces.

Although Hiramatsu and colleagues' (2017) data provide initial support for a social evolutionary account of trichromatic color vision, some methodological issues prohibit drawing conclusions with regard to human interaction. Although proceptivity is an important characteristic for male rhesus macaques to identify in females, humans experience and exhibit a much more complex range of social states and emotions, and the degree to which trichromatic (vs. dichromatic) color vision influences judgments of these states and emotions remains unknown. Second, facial coloration differences within and outside of the proceptive behavioral period for rhesus macaques are likely to be much greater than facial coloration appearance changes that occur within humans. In other words, the differences in facial coloration that participants viewed in Hiramatsu et al.'s (2017) study were much more conspicuous than would be expected in human interaction. Examining how judgments of socially relevant variables differ as a function of trichromatic/dichromatic vision across subtle, real-life skin color appearance variations therefore seems essential. Third, one of the photographs in each trial of the Hiramatsu et al. (2017) study was objectively proceptive, and participants were provided with accuracy feedback in a series of practice trials as to which was the correct selection, essentially training participants to associate facial redness appearance with proceptivity. This type of feedback is unlikely to occur in human interactions. For example, people make snap judgments of socially relevant factors (e.g., health) without necessarily obtaining subsequent information to confirm or disconfirm their initial judgment.

The current research aims to extend our understanding of a social functional account of trichromatic color vision in humans. Our central focus is to manipulate human facial coloration in a manner consistent with a typical blushing response, simulate how this would be perceived by trichromatic versus dichromatic observers, and assess whether these low-level perceptual differences influence subsequent judgments of attractiveness, health, and emotion, each of which has important socially relevant consequences.

Previous work has demonstrated that computational modeling can be used to simulate what images would look like to dichromatic (and animal) observers, by adjusting the modeled cone sensitivities according to the missing photoreceptor (Brettel, Viénot, & Mollon, 1997; Hiramatsu et al., 2017; Melin, Kline, Hickey, & Fedigan, 2013; Viénot, Brettel, & Mollon, 1999; Viénot, Brettel, Ott, Ben M'Barek, & Mollon, 1995). We use this approach herein to generate image representations that simulate what the images would look like to routine trichromats (color-normal vision; sensitivity along three distinct L, M and S cones) and three dichromatic conditions: protanopia (missing sensitivity of L cone; red-green color deficiency), deuteranopia (missing sensitivity of M cone; red-green color deficiency), and tritanopia (missing sensitivity of S cone; blue-yellow color deficiency). We used two sets of faces: baseline (unmanipulated) faces, and the same faces manipulated to have increased skin lightness (CIELAB L* + 0.23), redness (CIELAB a* + 5.43), and yellowness (CIELAB b* + 1.88). These color values were obtained from previous data (Thorstenson, 2017) by measuring a hyperemic skin response (increased blood perfusion beneath the skin), simulating a flushed face. In Experiment 1, we simultaneously presented the baseline and flushed faces in pairs for the four color vision conditions and asked participants to select the faces that looked more attractive, healthy, and angry. In Experiment 2, we used a similar experimental design, except that participants were asked to rate on a continuous scale how attractive, healthy, and angry the faces looked. For both experiments, we expected flushed faces (relative to baseline faces) to be perceived as more attractive, healthy, and angry in the trichromatic condition. In addition, we expected that the difference between these evaluations in baseline and flushed faces would be stronger in the trichromatic condition relative to the dichromatic conditions. Particularly, we expected to observe the greatest difference between the trichromatic and the two red-green color-deficient conditions (protanopia and deuteranopia).

For both experiments, all data exclusions, manipulations, and variables analyzed are reported, and data collection was completed prior to any analysis. All participants were unique; each individual only participated in one experiment. All analyses included only participants with color-normal vision, assessed by self-report at the end of each experiment; participants who reported a color vision deficiency were excluded from all analyses a priori. Sample size was determined by a simultaneous a priori consideration of power and expected participant availability. In both experiments, sample size (target $n = 67$) was determined a priori via power analysis (targeting .80 power to detect a $d = 0.35$ effect at $p < .05$ in a within-subjects design). We fell slightly short of this target for Experiment 1 ($n = 66$) but were able to slightly exceed it for Experiment 2 ($n = 81$), due to participant availability in both cases.

Experiment 1

Methods

Participants. Sixty-six (40 females, $M_{\text{age}} = 20.18$, $SD_{\text{age}} = 1.39$) students with color-normal vision at a university in the northeast United States participated in the experiment in exchange for extra course credit.

Stimuli. We chose eight facial images (four males, four females) to use in the experiment. In the perceived health and attractiveness blocks, four images consisted of composite blends of multiple facial photographs with neutral expressions, resulting in four unique target identities. In the perceived anger block, four images were standardized photographs posing anger expressions, validated by past research to reliably elicit perceptions of anger (Radboud Faces Database; Langner et al., 2010).

The color appearance manipulations chosen for the current work were taken from previously measured data (Thorstenson, 2017). In this prior work, radiance measurements were taken from the skin of six Caucasian participants and from the source illuminant using a PR655 Spectroradiometer during two physiological periods (occlusion, when blood flow was blocked from the skin; hyperemia, when blood flow rapidly reentered the skin). The spectral reflectance of the skin was derived from the radiance measurements and then computed into CIELAB colorspace. Finally, the average colorimetric difference between the two measured physiological periods was calculated.

MATLAB was used to manipulate facial color appearance consistent with hyperemic skin to simulate an exaggerated flush response. This resulted in a baseline face image and a face image with increased facial lightness ($\Delta L^* = +0.23$), redness ($\Delta a^* = +5.43$), and yellowness ($\Delta b^* = +1.88$) in CIELAB colorspace. Photoshop was used to create face-shaped masks to ensure that the color changes were restricted to the skin areas of the face (i.e., excluded hair, eyes, teeth, clothing, and background). We then used open-source software (Wickline, 2000) to generate stimuli that simulate what the images would look like to routine trichromats (color-normal vision, sensitivity along L, M, and S cones; equivalent to the original images) and three dichromatic conditions: protanopia (missing L-cone sensitivity; simulating red-green color deficiency), deuteranopia (missing M-cone sensitivity; simulating red-green color deficiency), and tritanopia (missing S-cone sensitivity; simulating blue-yellow color deficiency). See Figure 2 for an example of the stimuli used in both experiments.

Procedure. Participants completed the experiment in a laboratory on a BenQ 24-in HD LED Color Certified monitor.

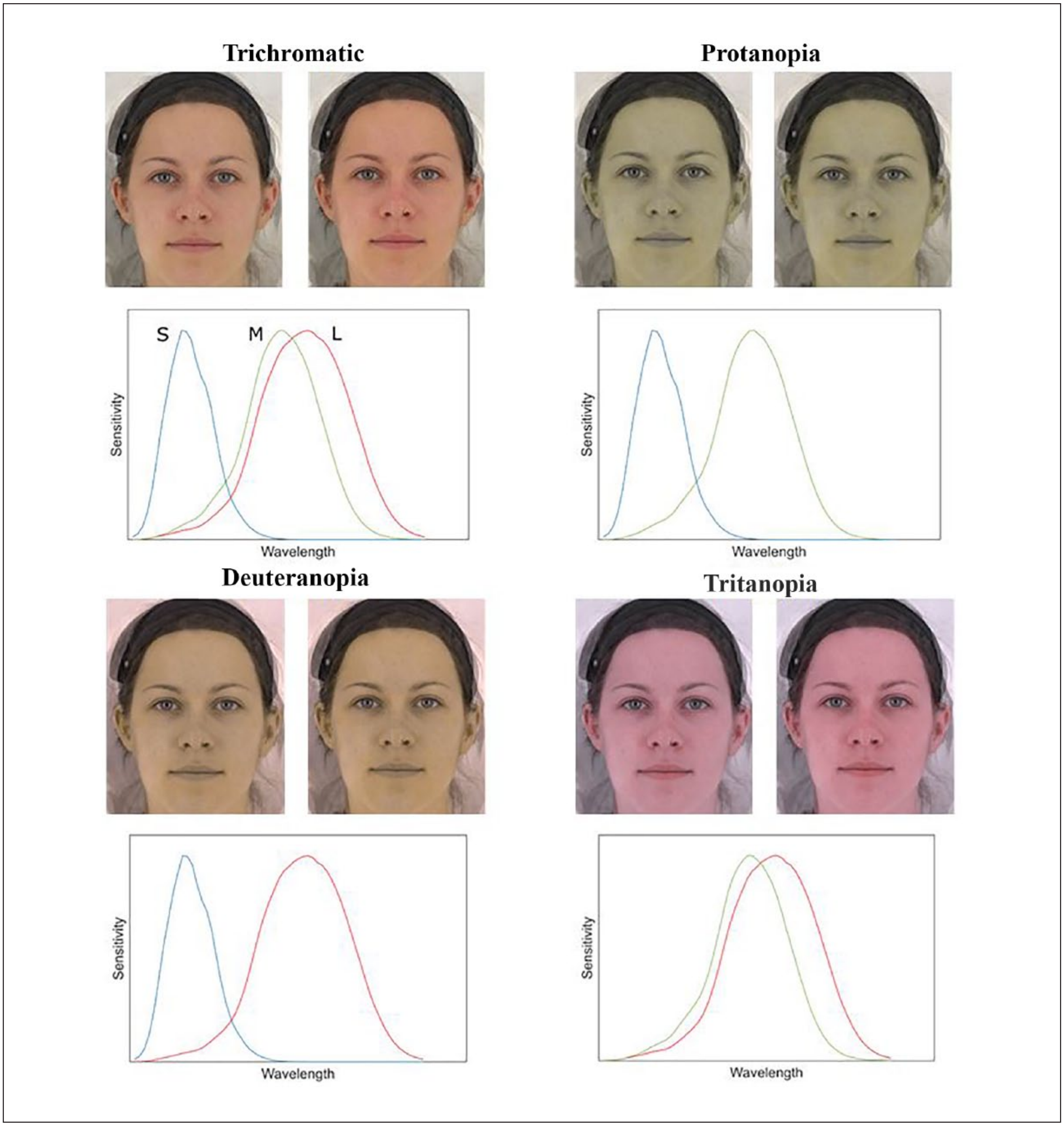

Figure 2. Example stimuli used in both experiments for health and attractiveness judgments. Baseline (left) versus flushed (right) faces simulated for the four color vision conditions.

Note. Below face images are the normalized spectral sensitivity functions for S (blue), M (green), and L (red) cones. Routine trichromats have differentiated spectral sensitivity for three cones, whereas protanopes are missing sensitivity for the L cone, deuteranopes are missing sensitivity for the M cone, and tritanopes are missing sensitivity for the S cone.

An Xrite i-one pro spectrophotometer was used to color-calibrate the display (achieved monitor specifications were D65, $x = 0.31$, $y = 0.33$, $Y = 120$ cd/m^2, $\gamma = 2.2$, $\Delta E_{\text{Mean}} = 0.259$). The viewing distance was approximately 55 cm and the viewing angle was approximately 0° to 15°. The display background was white, and the monitor surround was black. The room was dimly lit. Participants viewed each pair of faces (baseline vs. flushed) simultaneously and were asked to make a social evaluation by choosing one of the faces (two-alternative forced-choice [2AFC]). Participants were asked, "Which face looks more healthy [attractive, angry]?" Participants viewed and chose between each pair of faces (four per block), for each block (perceived health, attractiveness, anger), in each of the four color conditions (trichromatic, protanopia, deuteranopia, tritanopia), for a total of 48 trials. Block order, image-pair order within blocks, and presentation (flush image left vs. right) were randomized.

Results

Composite scores were created by averaging face selections (coded baseline = 0, flushed = 1) separately for target sex, evaluation block, and color condition, representing the proportion of flushed selections to baseline selections made by participants.

A 2 (target sex: male, female) × 3(evaluation: health, attractiveness, anger) × 4 (color condition: trichromatic, protanopia, deuteranopia, tritanopia) repeated-measures ANOVA was conducted to evaluate the influence of target sex, evaluation, and color condition on facial baseline versus flushed image selections. There were no significant main or interactive effects of target sex, so this model was reduced to a 3 (evaluation) × 4 (color condition) repeated-measures ANOVA.

There was a significant Evaluation × Color Condition interaction, $F(6, 360) = 2.832$, $p = .010$, suggesting that the influence of color condition on face selections varied as a function of evaluation. We next proceed to investigate this influence for each evaluation separately.

Perceived health. For perceived health evaluations, there was a main effect of color condition, $F(3, 195) = 18.231$, $p < .001$. Flushed faces were more likely to be selected relative to baseline faces in the trichromatic condition ($M = 0.670$, $SE = 0.042$) versus the protanopia ($M = 0.386$, $SE = 0.033$), $t(65) = 5.29$, $p < .001$, $d = 0.65$, $\mathrm{CI}_{\mathrm{diff}} = [0.177, 0.391]$, and deuteranopia ($M = 0.473$, $SE = 0.032$), $t(65) = 4.48$, $p < .001$, $d = 0.55$, $\mathrm{CI}_{\mathrm{diff}} = [0.109, 0.285]$, conditions. There were no significant differences in face selections between the trichromatic and tritanopia ($M = 0.659$, $SE = 0.039$) conditions, $t(65) = 0.31$, $p = .761$, or between the protanopia and deuteranopia conditions, $t(65) = 1.87$, $p = .066$ (although this comparison is marginally significant). One-sample t tests against a test value of 0.5 (chance) were conducted to assess whether participants selected flushed faces more often than baseline faces to indicate perceived health at greater-than-chance level. Flushed faces were more likely to be selected relative to baseline faces in the trichromatic, $t(65) = 4.071$, $p < .001$, $d = 1.01$, $\mathrm{CI}_{\mathrm{diff}} = [0.087, 0.254]$, and tritanopia, $t(65) = 4.062$, $p < .001$, $d = 1.01$, $\mathrm{CI}_{\mathrm{diff}} = [0.081, 0.237]$, conditions. Conversely, flushed faces were less likely to be selected relative to baseline faces in the protanopia condition, $t(65) = 3.407$, $p = .001$, $d = 0.85$. Flushed relative to baseline face selections were not significantly different from chance level in the deuteranopia condition, $t(65) = 0.829$, $p = .41$.

Attractiveness. For attractiveness evaluations, there was a main effect of color condition, $F(3, 192) = 3.264$, $p = .023$. Flushed faces were more likely to be selected relative to baseline faces in the trichromatic condition ($M = 0.581$, $SE = 0.040$) versus the protanopia ($M = 0.458$, $SE = 0.031$), $t(65) = 2.45$, $p = .017$, $d = 0.30$, $\mathrm{CI}_{\mathrm{diff}} = [0.023, 0.224]$, and deuteranopia ($M = 0.458$, $SE = 0.032$), $t(65) = 2.20$, $p = .031$, $d = 0.27$, $\mathrm{CI}_{\mathrm{diff}} = [0.011, 0.235]$, conditions. There were no significant differences in face selections between the trichromatic and tritanopia ($M = 0.542$, $SE = 0.041$) conditions, $t(65) = 1.03$, $p = .306$, or between the protanopia and deuteranopia conditions, $t(65) = 0.0$, $p = 1.00$. One-sample t tests against a test value of 0.5 (chance) were conducted to assess whether participants selected flushed faces more often than baseline faces to indicate attractiveness at greater-than-chance level. Flushed faces were more likely to be selected relative to baseline faces in the trichromatic, $t(65) = 2.041$, $p = .045$, $d = 0.50$, $\mathrm{CI}_{\mathrm{diff}} = [0.002, 0.160]$, condition. Flushed relative to baseline face selections were not significantly different from chance level in the protanopia, $t(65) = 1.069$, $p = .289$, deuteranopia, $t(65) = 1.04$, $p = .302$, or tritanopia, $t(65) = 1.206$, $p = .232$, condition.

Perceived anger. For perceived anger evaluations, there was a main effect of color condition, $F(3, 195) = 15.323$, $p < .001$. Flushed faces were more likely to be selected relative to baseline faces in the trichromatic condition ($M = 0.746$, $SE = 0.039$) versus the protanopia ($M = 0.538$, $SE = 0.032$), $t(65) = 4.43$, $p < .001$, $d = 0.55$, $\mathrm{CI}_{\mathrm{diff}} = [0.115, 0.302]$, and deuteranopia ($M = 0.511$, $SE = 0.033$), $t(65) = 5.49$, $p < .001$, $d = 0.68$, $\mathrm{CI}_{\mathrm{diff}} = [0.149, 0.320]$, conditions. There were no significant differences in face selections between the trichromatic and tritanopia ($M = 0.708$, $SE = 0.041$) conditions, $t(65) = .94$, $p = .353$, or between the protanopia and deuteranopia conditions, $t(65) = 0.69$, $p = .49$. One-sample t tests against a test value of 0.5 (chance) were conducted to assess whether participants selected flushed faces more often than baseline faces to indicate perceived anger at greater-than-chance level. Flushed faces were more likely to be selected relative to baseline faces in the trichromatic, $t(65) = 6.356$, $p < .001$, $d = 1.58$, $\mathrm{CI}_{\mathrm{diff}} = [0.169, 0.324]$, and tritanopia, $t(65) = 5.131$, $p < .001$, $d = 1.27$, $\mathrm{CI}_{\mathrm{diff}} = [0.127, 0.289]$, conditions. Flushed relative to baseline face selections were not significantly different from chance level in the protanopia, $t(65) = 1.166$, $p = .248$, or deuteranopia, $t(65) = .340$, $p = .735$, condition. See Figure 3 for a summary of the results from Experiment 1.

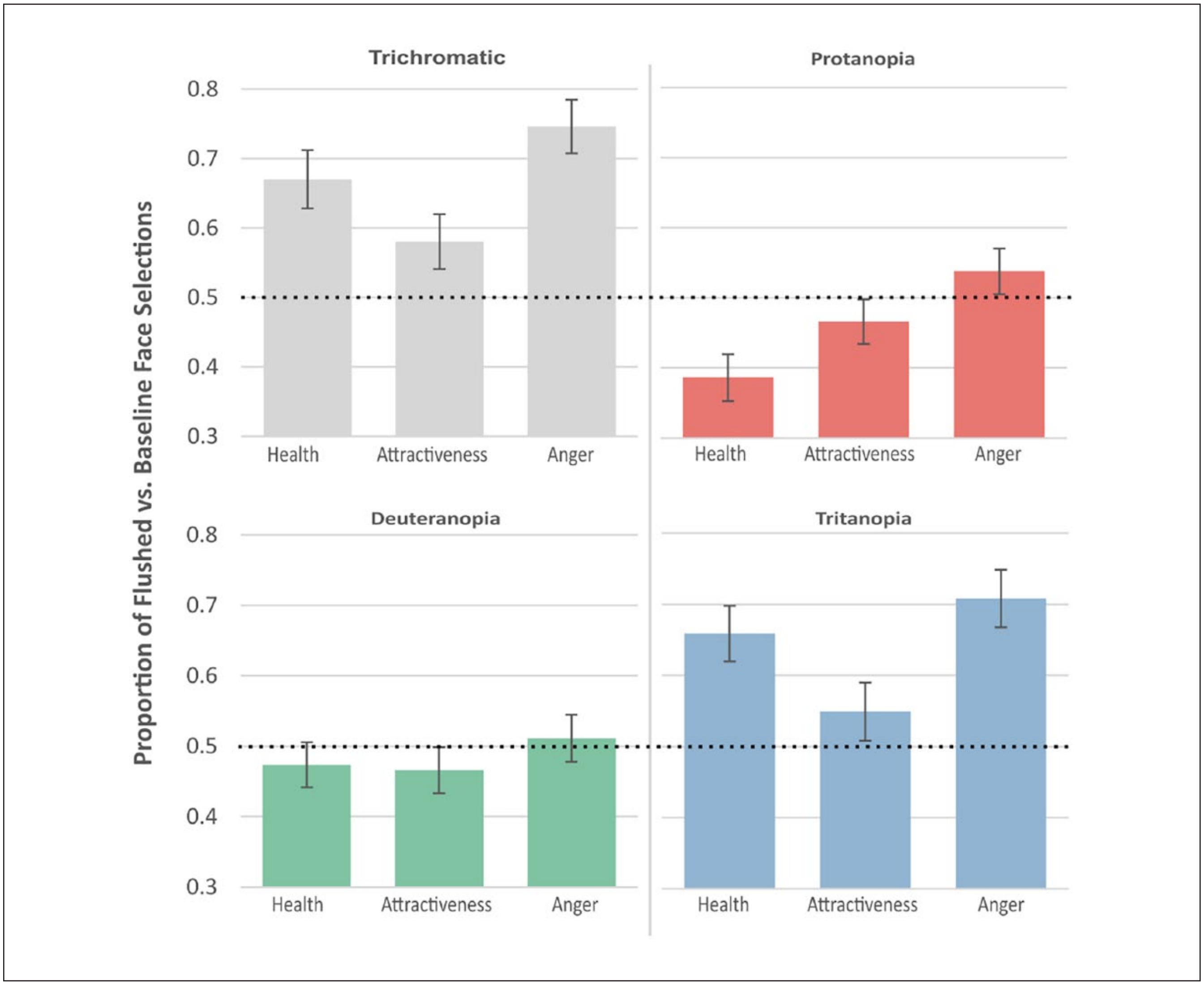

Figure 3. Summary of results from Experiment 1.

Note. Mean and standard error of flushed (relative to baseline) face selections as a function of evaluation and color condition. Participants were more likely to select flushed faces to indicate their social evaluations for trichromatic and tritanopia conditions, but not for deuteranopia and protanopia conditions. The dotted line represents chance level (0.5) for selecting flushed relative to baseline faces.

Experiment 2

Methods

Eighty-one (41 females, $M_{\text{age}} = 20.25$, $SD_{\text{age}} = 1.52$) students with color-normal vision at a university in the northeast United States participated in the experiment in exchange for extra course credit. The stimuli and procedure were identical to those used in Experiment 1, with the exception that participants rated each face on evaluations using a slider ("How healthy [attractive, angry] does this person look?" from 1 = *not at all* to 9 = *very much*), instead of a forced-choice design. Participants completed the experiment in a laboratory on the same monitor, color-calibrated using the same specifications as in Experiment 1.

Results

Composite scores were computed by averaging participants' ratings, separately across face images (within color pairs), evaluations, and color conditions. A 3 (evaluation: health, attractiveness, anger) × 2 (face color: baseline, flushed) × 4 (color condition: trichromatic, protanopia, deuteranopia, tritanopia) repeated-measures ANOVA was conducted to evaluate the influence of evaluation, face color, and color condition on participants' ratings.

A significant three-way interaction between evaluations, face color, and color condition emerged, $F(6, 480) = 2.871$, $p = .009$, indicating that the influence of face color on ratings varied as a function of evaluation type and color condition. We proceed to explore this interaction by testing color

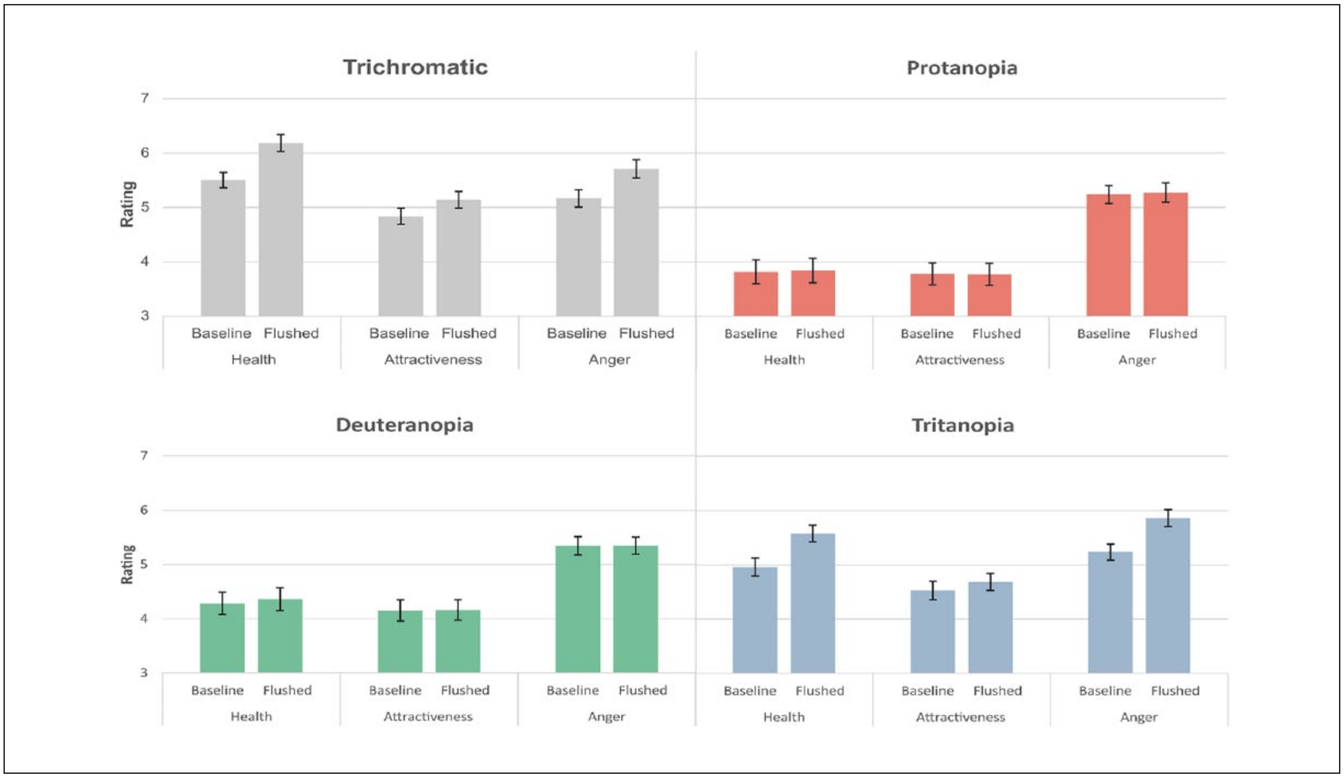

Figure 4. Summary of results from Experiment 2.

Note. Mean and standard error of baseline versus flushed face ratings as a function of evaluation and color condition. Flushed faces were perceived as more healthy, attractive, and angry for both trichromatic and tritanopia conditions, but not for protanopia or deuteranopia conditions.

condition and face color effects separately for each evaluation type.

Perceived health. Flushed faces (M = 6.188, SE = 0.156) were perceived as healthier than baseline faces (M = 5.506, SE = 0.142) in the trichromatic condition, $t(80) = 5.849$, $p < .001$, $d = 0.65$, $\mathrm{CI}_{\mathrm{diff}} = [0.450, 0.914]$. In addition, flushed faces (M = 5.577, SE = 0.152) were perceived as healthier than baseline faces (M = 4.957, SE = 0.165) in the tritanopia condition, $t(80) = 5.256$, $p < .001$, $d = 0.58$, $\mathrm{CI}_{\mathrm{diff}} = [0.386, 0.855]$. There were no significant differences in perceived health between flushed and baseline faces in the protanopia, $t(80) = .299$, $p = .766$ ($M_{\mathrm{flushed}} = 3.843$, $SE_{\mathrm{flushed}} = 0.225$; $M_{\mathrm{baseline}} = 3.818$, $SE_{\mathrm{baseline}} = 0.218$), or deuteranopia, $t(80) = 1.341$, $p = .184$ ($M_{\mathrm{flushed}} = 4.361$, $SE_{\mathrm{flushed}} = 0.209$; $M_{\mathrm{baseline}} = 4.284$, $SE_{\mathrm{baseline}} = 0.203$), conditions.

Attractiveness. Flushed faces (M = 5.142, SE = 0.152) were perceived as more attractive than baseline faces (M = 4.840, SE = 0.148) in the trichromatic condition, $t(80) = 4.384$, $p < .001$, $d = 0.65$, $\mathrm{CI}_{\mathrm{diff}} = [0.165, 0.440]$. In addition, flushed faces (M = 4.685, SE = 0.155) were perceived as more attractive than baseline faces (M = 4.528, SE = 0.168) in the tritanopia condition, $t(80) = 1.984$, $p = .051$, $d = 0.22$, $\mathrm{CI}_{\mathrm{diff}} = [–0.001, 0.315]$ (although this comparison was marginally significant). There were no significant differences in perceived attractiveness between flushed and baseline faces in the protanopia, $t(80) = 0.102$, $p = .919$ ($M_{\mathrm{flushed}} = 3.772$, $SE_{\mathrm{flushed}} = 0.205$; $M_{\mathrm{baseline}} = 3.778$, $SE_{\mathrm{baseline}} = 0.200$) or deuteranopia, $t(80) = 0.164$, $p = .87$ ($M_{\mathrm{flushed}} = 4.160$, $SE_{\mathrm{flushed}} = 0.189$; $M_{\mathrm{baseline}} = 4.151$, $SE_{\mathrm{baseline}} = 0.196$) condition.

Perceived anger. Flushed faces (M = 5.710, SE = 0.166) were perceived as angrier than baseline faces (M = 5.167, SE = 0.159) in the trichromatic condition, $t(80) = 4.783$, $p < .001$, $d = 0.53$, $\mathrm{CI}_{\mathrm{diff}} = [0.317, 0.769]$. In addition, flushed faces (M = 5.864, SE = 0.156) were perceived as angrier than baseline faces (M = 5.235, SE = 0.148) in the tritanopia condition, $t(80) = 5.794$, $p < .001$, $d = 0.64$, $\mathrm{CI}_{\mathrm{diff}} = [0.413, 0.846]$. There were no significant differences in perceived anger between flushed and baseline faces in the protanopia, $t(80) = .397$, $p = .693$ ($M_{\mathrm{flushed}} = 5.275$, $SE_{\mathrm{flushed}} = 0.177$; $M_{\mathrm{baseline}} = 5.241$, $SE_{\mathrm{baseline}} = 0.164$) or deuteranopia, $t(80) = 0.075$, $p = .94$ ($M_{\mathrm{flushed}} = 5.349$, $SE_{\mathrm{flushed}} = 0.157$; $M_{\mathrm{baseline}} = 5.343$, $SE_{\mathrm{baseline}} = 0.164$) condition. See Figure 4 for a summary of the results from Experiment 2.

The results from Experiment 2 showed a pattern such that flushed faces (vs. baseline faces) were perceived as more healthy, attractive, and angry in the trichromatic and tritanopia conditions, but not in the protanopia or deuteranopia condition. To evaluate whether these patterns were different between trichromatic and tritanopia conditions, we conducted a 3 (evaluation: health, attractiveness, anger) × 2 (face color: baseline, flushed) × 2 (color condition: trichromatic, tritanopia) repeated-measures ANOVA. There was no significant two-way interaction between face color and color condition, $F(1, 80) = 0.45, p = .504$, nor a significant three-way interaction between evaluation, face color, and color condition, $F(2, 160) = 1.527, p = .220$, indicating that the difference between face color ratings did not vary as a function of trichromatic versus tritanopia conditions.

General Discussion

In both experiments, participants perceived flushed (vs. baseline) faces as more attractive, healthy, and angry in the trichromatic condition. Furthermore, the difference in evaluations between baseline and flushed faces was more evident in the trichromatic, relative to the protanopia and deuteranopia conditions, but not relative to the tritanopia condition. These findings demonstrate a trichromatic color vision advantage (relative to particular dichromatic conditions) for social perception using stimuli that directly model a physiological aspect of skin appearance (i.e., flushing due to oxygenated blood flow). Importantly, our research design utilized human targets and human perceivers, manipulated facial color appearance in a manner similar to how facial color changes in real life, and assessed socially relevant outcome variables. We view these studies as providing supportive empirical evidence for the social evolutionary account of trichromatic color vision.

While we expected performance to be impaired in the tritanopia condition relative to the trichromatic condition, the differences between these conditions were not statistically significant across studies. This could be explained by evaluating the color appearance differences used in the current research to simulate the flushed faces. Flushed faces were adjusted to increase in lightness ($L^* + 0.23$), redness ($a^* + 5.43$), and yellowness ($b^* + 1.88$). While these color appearance changes were chosen based on previously measured data to accurately simulate a skin blood perfusion response, it is clear that the majority of the change occurs along the redness dimension. While protanopes and deuteranopes should not be able to distinguish between small changes in redness (due to missing sensitivity from either L or M cones, respectively), tritanopes should still be able to use the information from the redness dimension to make their evaluations. Similarly, in related research (Hiramatsu et al., 2017), performance in the tritanopia condition was closer to performance in the routine trichromatic condition than performance in the other dichromatic conditions. Finally, the evolution of trichromacy involved the duplication and divergence of the L/M cone, such that trichromats benefit from the three separate S, M, and L cones (while protanopes and deuteranopes possess an S cone along with a single L/M cone). Therefore, the comparisons between trichromats, protanopes, and deuteranopes (excluding tritanopes that enjoy both an L and M cone) more accurately represent a test of trichromatic evolutionary differences.

The current findings suggest that facial color appearance plays an important role in the perception of attractiveness, health, and emotion, which represent important interpersonal evaluations that guide social interaction and decision making. The findings are also consistent with predictions from an ecological theory of social perception (Zebrowitz-McArthur & Baron, 1983), namely that for social signals to be meaningfully transferred, there must be convergence between the stimulus information and the perceptual system. In the case of certain dichromatic conditions (protanopia, deuteranopia), the simulated perceptual system did not allow for discrimination of the facial flushing information, and therefore did not affect the social perceptions. Although the prevalence of dichromatic individuals in the general population is quite low (between 2% and 8% of males and approximately 0.4% of females have a red-green color deficiency, and approximately 0.002% of both males and females have a blue-yellow color deficiency; Birch, 2012; Simunovic, 2010), these findings raise the possibility that certain color deficiencies exhibit less informed decision making in the social domain as a consequence of systematic misperception. For example, dichromats may be less accurate at detecting others' emotional states, especially when facial expressions can be controlled (e.g., an angry person can maintain a neutral expression, but will still experience facial flushing). This may have problematic behavioral implications, such as failing to avoid someone with a flaring temper and a straight face. Dichromats may also display weaker approach/avoidance behavior toward healthy/sick individuals, and in the medical domain, it has been noted that dichromatic clinicians have significant difficulty in assessing clinically relevant skin color modulations (Changizi & Rio, 2010). Although empirical investigations into these possibilities would be difficult due to the relatively low prevalence of dichromats, they would be extremely informative nonetheless.

In both our review of extant literature and our current methodological approach, we conceptualize the perceptual phenomenon of color in accord with contemporary models of color vision. Specifically, CIELAB colorspace was modeled after the human visual system, describing color using three continuous, orthogonal dimensions: L^* (a lightness axis), a^* (a color-opponent red-green axis), and b^* (a color-opponent yellow-blue axis). Therefore, when describing, for example, an "increase in facial redness," we implicitly refer to a positive unit change along the CIELAB a^* axis. Furthermore, CIELAB was designed to be perceptually uniform, meaning that a unit change along one of the orthogonal dimensions is perceptually equivalent to the same unit change along another dimension, making it a well-suited visual space to systematically manipulate and assess color perception (Brainard, 2003; Fairchild, 2013). Yet, alternative ways to conceptualize and describe color appearance exist (e.g., LMS, CIE XYZ, CMYK, Munsell; see Fairchild, 2013; Tkalcic & Tasic, 2003). Importantly, researchers must consider their specific research question when deciding how to best conceptualize and describe color appearance (see Thorstenson, 2018).

It is worth noting that the current research presents (to color-normal observers) images that only simulate what dichromats likely see, using computational visual modeling techniques. However, the current data are unable to address what the images might look like to observers with lifelong dichromatic experience. Such observers might employ compensatory strategies to account for diminished chromatic discrimination, such as attending more to achromatic information, or might exhibit long-term adaptation or contrast gains either in the cones or through post-photoreceptor mechanisms (Melin et al., 2013). Future research could benefit from assessments that test real dichromatic observers. Furthermore, in the current research we solely manipulated skin color appearance to simulate facial color changes that occur in states related to attractiveness, health, and anger. However, other facial features are likely modified by similar states. For instance, face shape may also vary across the ovulatory cycle or due to healthy behaviors, and there are clearly structural modifications associated with emotion (e.g., facial-muscular expressions of emotion). In other words, color changes are not the sole way a face may convey important social states, although facial color might convey important information that cannot be conveyed by other modalities (see Thorstenson, Pazda, et al., 2018).

It is additionally important to note that the social perception hypothesis (i.e., that trichromatic color vision evolved with the adaptive function of serving the detection and discrimination of socially relevant states in others; Changizi et al., 2006) and the foraging hypothesis (i.e., that trichromatic color vision evolved with the adaptive function of serving foraging behaviors by detecting ripe fruit against green leaves; Allen, 1879; Mollon, 1989) are not mutually exclusive; these hypotheses may be considered simultaneously. For example, it may be the case that trichromacy initially evolved to serve other adaptive functions and was later co-opted to facilitate disparate roles (Regan et al., 2001).

Finally, the current work demonstrates the empirical utility of integrating social perception and visual perception methods. The emerging field of social psychophysics (see Jack & Schyns, 2017) approaches the complex challenge of identifying the precise lower level perceptual features that inform social evaluations by applying classic psychophysical techniques to address social perception questions. The current work utilizes this approach by demonstrating the receiver characteristics necessary for facial color appearance's influence on social evaluation (see also Thorstenson, 2018).

In sum, the current work provides supportive empirical evidence that the evolution of trichromacy confers an advantage for detecting important social information conveyed through facial color appearance. This work highlights the role of facial color in nonverbal social communication, the influence of facial color on social perception, the possible role of skin color in trichromatic evolution, and the broader utility of integrating social perception and visual perception research.

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Supplemental Material

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