Supplementary Materials

[for Changizi, Zhang and Shimojo, “Bare skin, blood, and the evolution of primate color vision.”]

1. Supplementary extended legend for Figure 1 of main paper

The skin spectra in Figure 1c and 1d utilize an analytical physics model (Zonios et al., 2001), with the following parameter settings: melanin content = 10^{-4} mmol/liter, hemoglobin concentration in the blood = 2.32, reduced scattering coefficient = 1.5 mm^{-1}, and scattering size = 0.5 μm. Our variations of oxygen saturation ranged over three values, 25% (“deoxy”), 75% (“baseline”) and 100% (“oxy”), and hemoglobin skin concentration over 0.5% (“low blood”), 1% (“baseline”) and 2% (“high blood”). In computing the cone responses for Figure 1d, we used illuminant D65, 2° cone fundamentals (Stockman & Sharpe, 2000), and human macular pigment density and lens density spectra (Bone et al., 1992; Stockman et al., 1999). These spectral data are obtainable from the the web site of A. Stockman and L. T. Sharpe, Color and Vision Research Laboratories, Institute of Opthalmology (http://cvrl.ioo.ucl.ac.uk/). Once the S, M and L cone activations were computed, we computed u = L-M and v = S-(L+M). We are interested in the shift in these values from the baseline skin, and this was computed as $u_{norm} = (u-u_{base})/abs(u_{base})$, and $v_{norm} = (v-v_{base})/abs(v_{base})$. In Figure 2d we denote these as $(L-M)_{norm}$ and $S-(L+M)_{norm}$. The photographs in Figure 1e are of skin from the second author’s palm, and they are approximately placed in color space according to their color deviation from baseline. Baseline skin is shown in the center, skin with the blood manually pressed out becomes yellowed and is shown on the bottom, skin after several minutes of tourniquet acquires a significant increase in blood concentration, and becomes purplish, which is on the upper right of this color space, and the skin possessing underlying veins is modulated toward green-blue (the veins run roughly vertically through this photograph), and shown on the top left. [Note that skin with underlying veins seen through an aperture does not appear green-blue; the color is shifted toward green-blue, and appears green-blue when viewed with surrounding normal skin (Kienle, 1996).] The color space is a pseudo-opponent color space, normalized so that baseline skin is the zero point. It is computed as described above, but using RGB rather than LMS.

2. Supplementary discussion of evidence for perceptual sensitivity to skin color modulations

In addition to the M and L cone sensitivities being near-optimal for responding to skin spectral modulations, there is evidence that perception is indeed sensitive to these modulations. First, that humans are perceptually highly sensitive to skin color variation is widely appreciated by television engineers (Lee & Ha 1997), artists (Horton & Harrison 1995) and animators (Patel 1995), who know that skin color is one of the most difficult colors to render appropriately. Face recognition is color dependent to a much greater degree than is object-recognition more generally (Subramanian & Biederman, 1997; Tarr et al., 2001; Yip & Sinha, 2002; Russell et al., 2004). Consistent with maximum sensitivity to skin color changes (Kalish 1958, Honig & Urcuioli 1981), skin color (of one's own phenotype, at least) is very difficult to categorize. Of the 11 basic color terms across languages (Kay & Regier 2003) none apply well to skin. In fact, in OSA uniform color space there is only one conspicuous large region to which no basic color term applies, and in this region of color space lie the skin tones (Boynton & Olson 1987); the least color-categorizable position in OSA space is a skin tone within this region (Boynton 1997). In addition to the preceding evidence that humans are perceptually highly discriminating of skin colors, human dichromats are, as predicted, notoriously poor at such discriminations (Supplementary Table 1).

3. Supplementary discussion of skin bareness

An alternative potential explanation for the phenomenon that trichromats tend to be bare-faced is that because trichromats tend to be social (Allman, 1999), face recognition is important, and perhaps bare skin aids in face recognition. It is not obvious, however, that bare skin is such an aid; other mammals are able to recognize one another without bare skin (e.g., canines). A related alternative potential explanation is that non-color facial expressions are important for trichromats, and the recognition of such expressions is perhaps aided when the skin is bare. As for face recognition, it is not prima facie clear that bare skin is advantageous for non-color facial expression perception and discrimination, for fur can in principle help to accentuate the visibility of muscular movements (e.g., eye-lashes make eye-lid movements easier to see). We note that each of these potential alternative hypotheses are not inconsistent with bare skin also being crucial for color-signaling.

We note that we do not currently have an explanation for the high incidence of dichromacy in male humans (despite their possessing the least hair among catarrhine primates), nor can we (or frugivory and folivory hypotheses) explain the lack of trichromacy among male platyrrhines.

Finally, whether or not trichromacy was originally selected for the perception of skin color signaling, there are two possibilities concerning the evolution of face bareness. (1) Bare skin (e.g., on the face or rump) was selected for some other reason, after which trichromacy was useful for discriminating skin color modulations. (2) Trichromacy could have been mildly useful even on a lightly furry face, after which skin-color signaling could have been selected for, along with the gradual loss of fur. We currently know of no theoretical or empirical reason to favor one of these possibilities over the other.

4. Supplementary discussion of evidence concerning color modulations in primates and man

Does primate skin, in fact, perceptibly change in color as a function of mood or state? It is common knowledge that this is the case for many human phenotypes (Darwin, 1899). Non-human primates appear to undergo many of the same emotions as humans (Parr, 2003), and it has long been noticed that some primate faces undergo short-term color modulations with emotion (e.g., in Darwin, 1899; red with anger, p.

137; pale with terror, p. 144). More generally, non-human primates undergo skin color changes that are indicative of state (psychological or physical)—e.g., socio-sexual signals and threat displays—and these colors are perceived by conspecifics (e.g., Hingston, 1933; Wickler, 1967; Waitt et al., 2003).

Many human and non-human primates have darkly pigmented skin, and one may wonder how perceptible color modulations are in such cases. For example, in Figure 1a one can see that the "W" feature has a much lower amplitude for some skin (e.g., "East Indian (dark)") than for others, and perhaps will undergo less change as a function of oxygenation. Supplementary Figure 2 shows a variety of skin spectra from the NCSU skin spectrum database for East Indians, Asians, Africans and Caucasians, focusing on the "W" feature. One can see that the amplitude of the "W" feature is variable within each of these four human phenotypes, but that for each phenotype there are cases where the "W" feature is salient, suggesting that the feature is found universally across human phenotypes, albeit with variation within a phenotype. Furthermore, although darker skin diminishes the amplitude of the "W", the entire reflectance spectrum is also lower, and the amplitude of the "W" *relative* to the overall height of the reflectance spectrum does not significantly correlate with the lightness of skin (Supplementary Figure 3). That is, the salience of the "W" feature does not significantly correlate with the lightness of the skin.

In addition, there is evidence that blushes are visible on even very dark-skinned faces, although the blush appears different than that of a lighter-skinned person. Darwin writes, "Several trustworthy observers have assured me that they have seen on the faces of negroes an appearance resembling a blush, under circumstances which would have excited one in us, though their skins were of an ebony-black tint. Some describe it as blushing brown, but most say that the blackness becomes more intense." (Darwin, 1899, p. 318). Darwin follows this with, "It is asserted by four of my informants that the Australians, who are almost as black as negroes, never blush. A fifth answers doubtfully, remarking that only a very strong blush could be seen, on account of the dirty state of their skins. Three observers state that they do blush; Mr. S.

Wilson adding that this is noticeable only under a strong emotion, and when the skin is not too dark from long exposure and want of cleanliness. Mr. Lang answers, 'I have noticed that shame almost always excites a blush, which frequently extends as low as the neck.' " (Darwin, 1899, p. 319-320). Concerning such observations, one must recognize that many of these observers were white and probably raised in an environment where lighter skin was the normal baseline; we would expect such individuals to be less capable of discriminating skin color deviations around a dark-skinned baseline. For example, Darwin writes that "Von Spix and Martius, in speaking of the aborigines of Brazil, assert that they cannot properly be said to blush; 'it was only after long intercourse with the whites, and after receiving some education, that we perceived in the Indians a change of colour expressive of the emotions of their minds.' " (Darwin, 1899, p. 318). Although the implication is that the aborigine's education led to greater blushing, it is much more plausible that it was the whites' greater experience with aborigine skin color that trained them to perceive it.

Finally, we note that just as there is a large range of skin lightnesses in human (Jablonski & Chaplin, 2000), there is a large range for non-human primates (approximately one order of magnitude, Sumner & Mollon, 2003, Fig 5B, and also see the pictures in Supplementary Figure 1 here). Thus, although the ancestral human may have been dark-skinned, it is not clear what was the skin color for the ancestral trichromat. Even if very dark skin makes color modulations more difficult to perceive (something we provided some evidence against above), the ancestral trichromat may have lighter skin, after which some primates evolved darker skin.

5. Supplementary discussion of evidence concerning the association between color and mood/emotion

Sensitivity to modulations of the two blood variables is presumably selected for not because of a selective advantage to sensing changes in blood physiology per se, but because of the selective advantage of perceiving the associated emotional states or moods. Our hypothesis expects, therefore, that skin color modulations should have strong associations with emotional states. That this is true for humans is known informally to all of us; e.g., blushing with embarrassment, blanching with fear, and reddening with anger, and there is a long history of psychophysiological studies of emotion and its physiological correlates, including skin color modulations (Darwin 1899/1965; Sinha et al. 1992; Cacioppo et al. 1993; Drummond 1994; Levenson 2003). Color is sufficiently suggestive of emotion that cartoons often use color on a face to indicate emotional state (see Supplementary Figure 4). [Red clothing even appears to enhance human performance in Olympic combat sports (Hill & Barton, 2005).] Also, there are strong associative connections between color terms and emotion that hold across languages (Osgood 1960). In particular, for English many of the principal definitions of color terms refer explicitly to emotion (Supplementary Figure 5). And interestingly, many of the principal color definitions in English refer to skin and blood (Supplementary Figure 5), suggesting a strong connection between color, emotions, skin and blood. Our hypothesis may provide avenues for explaining enigmatic aspects of color, such as why some hues are considered across cultures to be warm (light) versus cold (dark), or strong versus weak (see Supplementary Figure 6).

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Supplementary Table 1

Evidence that human dichromats have difficulty perceiving skin modulations.

Citation	**Difficulty for color deficient observer**
PERSONAL OBSERVATIONS	
Dalton (1794) [discussed in Anthony & Spalding (2004)]	…could scarcely distinguish mud from blood on his stockings.
Wilson (1855) [discussed in Anthony & Spalding (1999, 2004)]	Problems recognizing redness in the lips, cheeks, nose, and inflammation, all which looked like blue. [A physician interviewed by Wilson.]
Best & Haenel (1880) [discussed in Anthony & Spalding (1999, 2004)]	Most struck by the change in normal people's complexion. Skin appeared waxen pale, with a hint of icterus, their lips and cheeks cyanosed and their opic discs very pale. [Haenel, a physician, induced temporary color deficiency in himself via snowblindness through snow skiing.]
Little (1881) [discussed in Anthony & Spalding (1999, 2004)	Difficulty recognizing inflammation in the eyes. Red appeared to him bluish; for example, in kerato-conjunctivitis and the retinal reflex. [An ophthalmologist.]
Ahlenstiel (1951)	"Slight reddening of the skin, as in blushing, is overlooked by the red-green blind. Growing pale is also overlooked, as is a very slight scarlet rash. Stronger reddening of the skin is labelled as dark grey shadow by the red-green blind. … Reddening of the interior parts of the body, in the throat, nose, ears and epiglottis, are more difficult to recognise. The bluish discolouration of the lips and nails in circulatory disorders remains imperceptible. Blood spots are imperceptible to the red-green blind on dark materials."
Logan (1977), Spalding (1993), Currier (1994) [discussed in Anthony & Spalding (1999, 2004)]	Difficulty recognizing blushing, pallor, faint rashes, cyanosis, erythema, blood in body products. [Difficulties common to four congenital color-deficient doctors.]
Jeffries (1983) [discussed in Anthony & Spalding (1999, 2004)]	Trouble recognizing the colour of throats ulcers, gangrene, and some sores. [A physician.]
Voke (1980) [discussed in Anthony & Spalding (1999)]	Identifying organs, the presence of pus, blood, cyanosis, jaundice, and facial discolouration. [Medical professionals.]
Cockburn (2004)	"As a child I could not understand what people meant when they said someone was blushing…" [first sentence of this paper!]. "…embarrassment when a patient complained of a red eye but the offending side…was not specified. …most severe problem was in differentiating between blood and pigment in the retina" [p. 351]. [An optometrist.]
Anthony & Spalding (2004), p. 345	"…I had failed to see the extreme pallor of a woman waiting for surgery. 'Anyone could see it,' the gynaecologist said but I could not. The operation was delayed for a week while the patient received a blood transfusion."
STUDIES	
Steward & Cole (1989), Cole (2004)	Difficulties recognizing skin rashes and sunburn. [17% of color deficient patients queried.]
Campbell et al. (1999)	Recognizing skin rashes, erythema, cyanosis, jaundice, blood in stool. [Among doctors.]
Spalding (1997, 1999)	Most common difficulties were recognizing body color changes of pallor, cyanosis, jaundice, and cherry red. Second commonest difficulty concerned recognizing rashes and erythema of skin. [Among doctors.]
Reiss et al. (2001)	Problems detecting blood in body fluids. [Among doctors.]

[Supplementary Table 1, Changizi et al., "…primate color vision…"]

References for Supplementary Table 1

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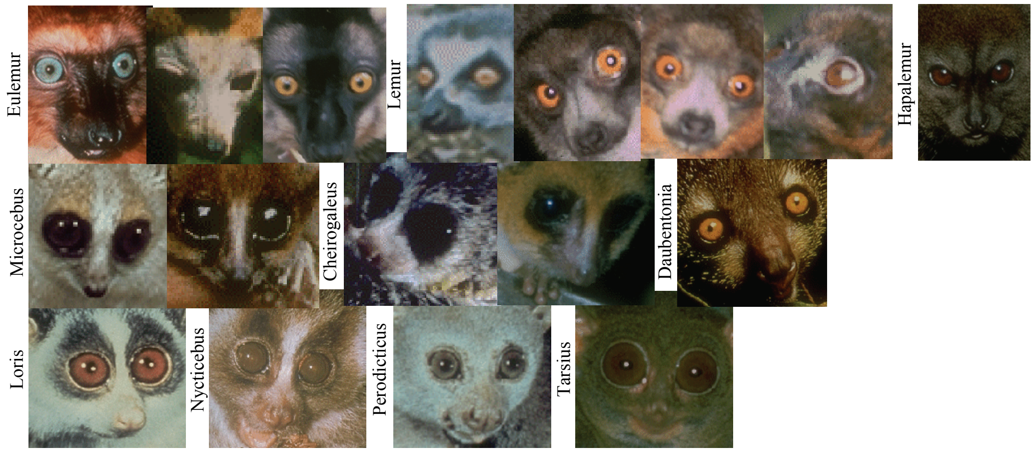
Supplementary Figure 1

Primates categorized by the kind of color vision: (**a**) monochromats, (**b**) dichromats, (**c**) polymorphic trichromats, (**d**) routine trichromats. (**e**) shows the bareness of primate faces as a function of the kind of color vision. Each empty circle shows the average bareness for species within a genus. The solid squares show the average (and standard error) bareness across the genera in each color group. Photographs are shown of one species of each genera in the color groups (their height on the plot not representative of anything). One can see from the pictures [(a) through (d)] and the plot [in (e)] that the monochromats and dichromats tend to be furry faced, and the trichromats (both polymorphic and routine) tend to have significant bare regions. These images are from National Primate Research Center, University of Wisconsin, Madison (http://pin.primate.wisc.edu/av/images/). Bareness was quantitatively estimated using these close-up images, and the percentage of bare skin projected onto the image determined within the region of the face bounded by the brows, and drawing straight lines on the photograph from the outer sides of the brows down to the sides of the chin [see the three photographs at the top of (e)]. Because the images shown at the National Primate Research Center have not been selected with our hypothesis in mind, these images provide an unbiased sample of primate images.

a Monochromats

b Dichromats



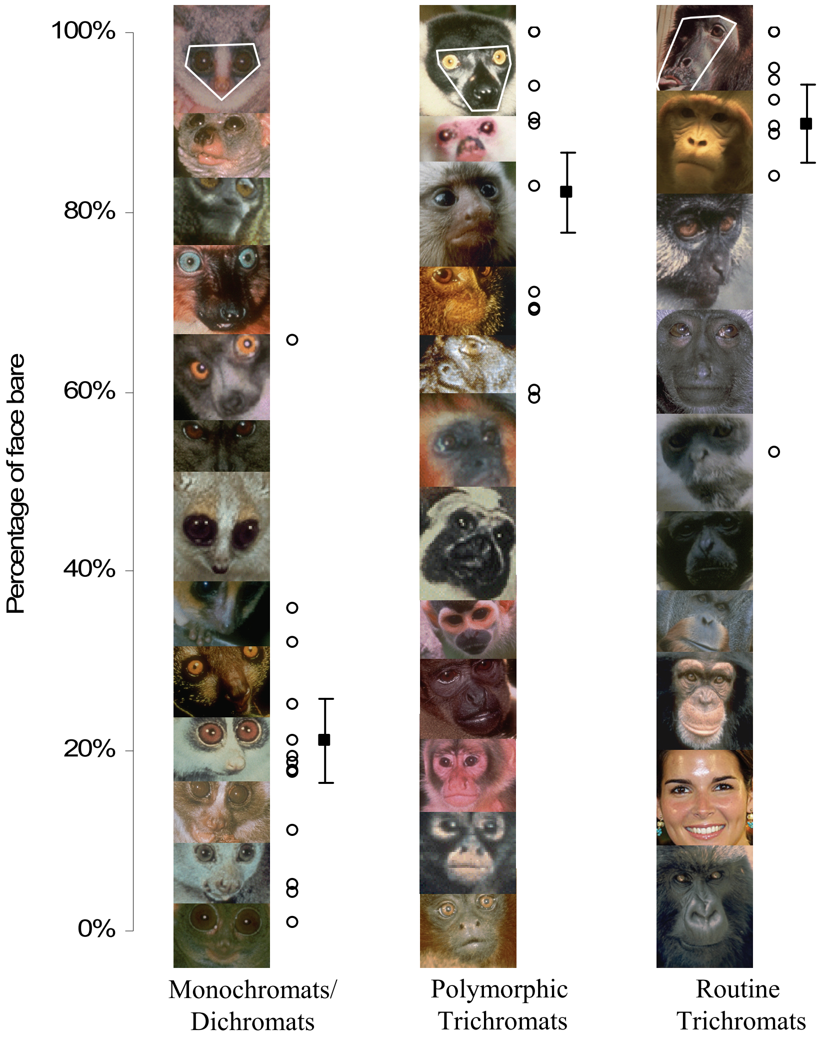
Supplementary Figure 1, Changizi et al., "…primate color vision…"

c Polymorphic Trichromats

d Routine Trichromats

Supplementary Figure 1, continued, Changizi et al., "…primate color vision…"

e



Supplementary Figure 1, continued, Changizi et al., "…primate color vision…"

Supplementary Figure 2

Reflectance spectra from human skin (taken from the NCSU spectral database) within the 500nm to 600nm range, focusing on the “W” feature. The y-axis in each case is the same scale. Also shown are “close ups” of the “W” feature for a male Mandrill (Sumner and Mollon, 2003). In nearly every case it is possible to see the “W” feature. For each human phenotype (African, Asian, East Indian and Caucasion), (i) there is considerable variability in the salience of the “W”, and (ii) there are cases in this database with a strong “W”, suggesting that the “W” feature is not peculiar to, or absent from, any of these phenotypes. The same can be found from other sources of skin spectral measurements, including Buck and Froelich (1948) and Angelopoulou (2001).

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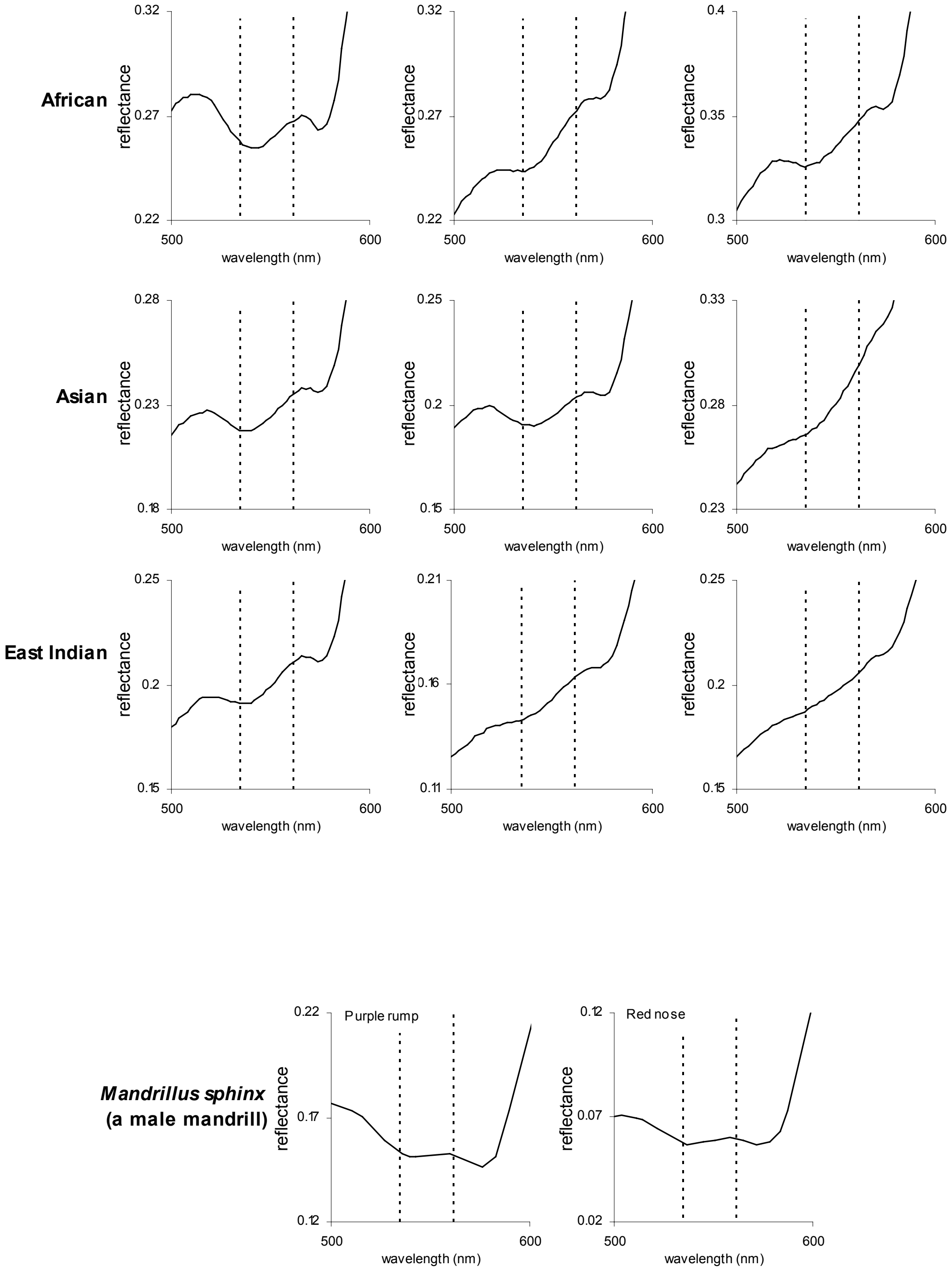
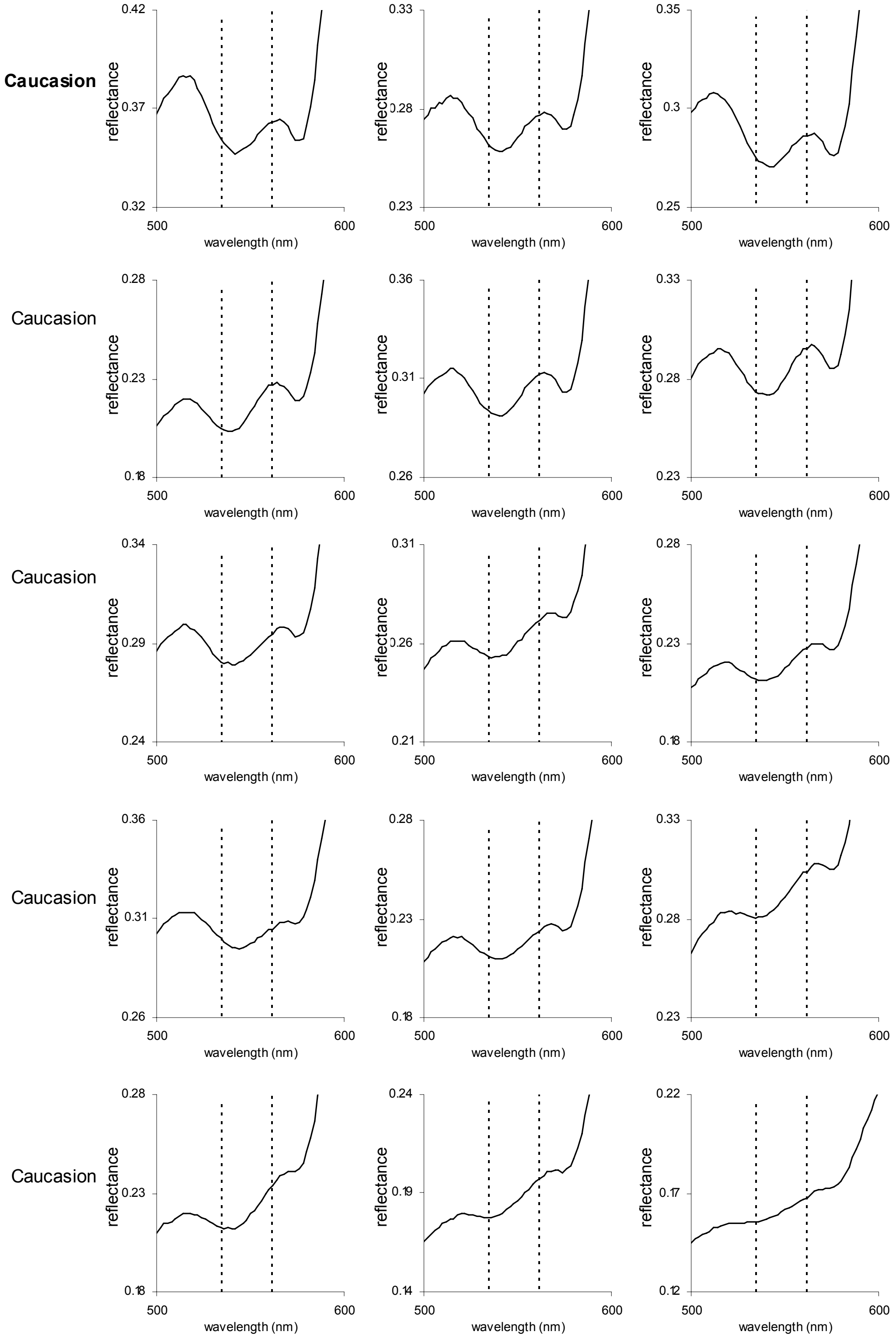


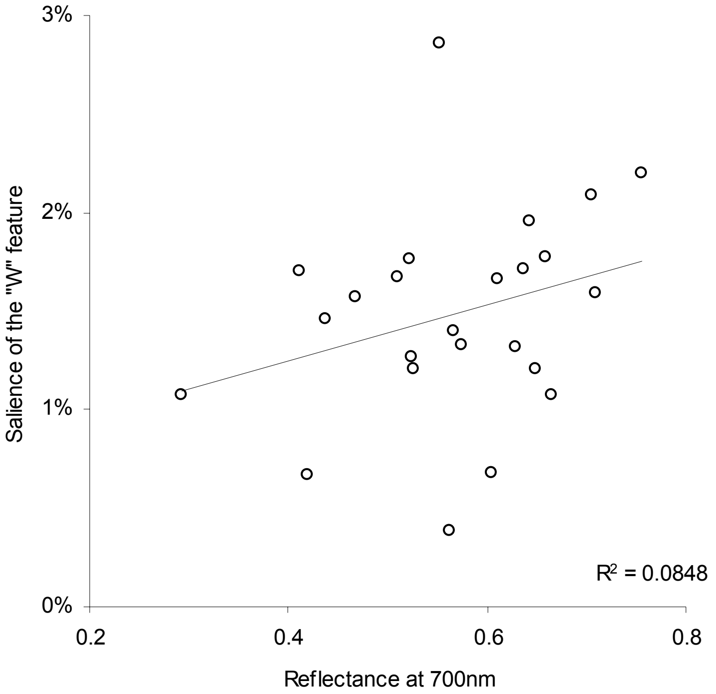
Supplementary Figure 2, Changizi et al., "…primate color vision…"



Supplementary Figure 2, continued, Changizi et al., "…primate color vision…"

Supplementary Figure 3

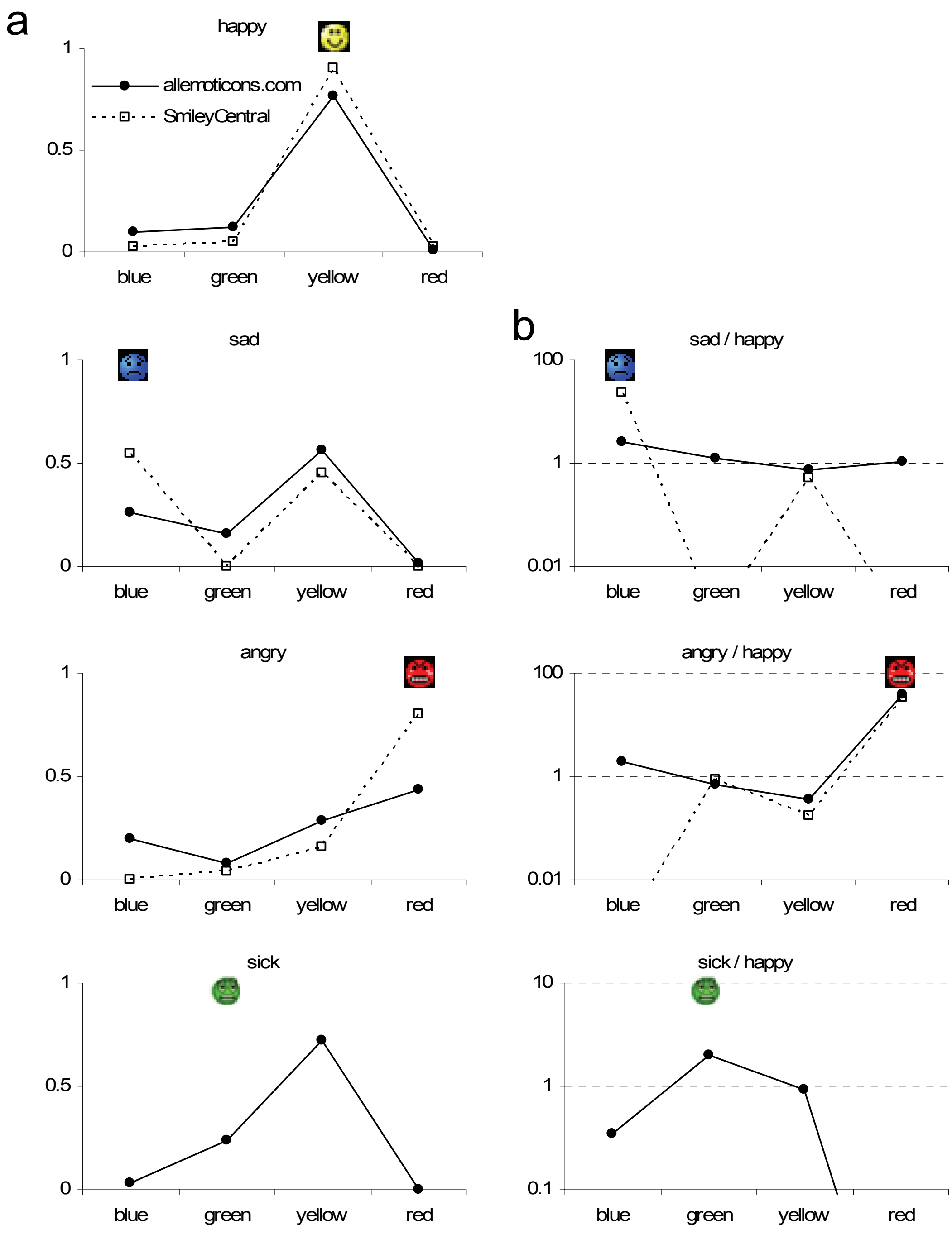
The salience of the “W” feature versus the skin reflectance at 700nm, for each of the human skin spectra from Supplementary Figure 1. The skin reflectance at 700nm serves as a measure of the overall height of the reflectance function. Salience of the “W” feature was measured as the difference between the “W” peak and the average of the two dips, divided by the reflectance at 700nm. Relativizing by the reflectance is appropriate because smaller cone modulations are increasingly perceptible at lower stimulus energies. The plot shows that more reflective skin does not tend to have a significantly more salient “W” feature ($R^2 = 0.85$, $df = 22$, $t = 1.43$, $p \approx 0.1$).



Supplementary Figure 3, Changizi et al., "…primate color vision…"

Supplementary Figure 4

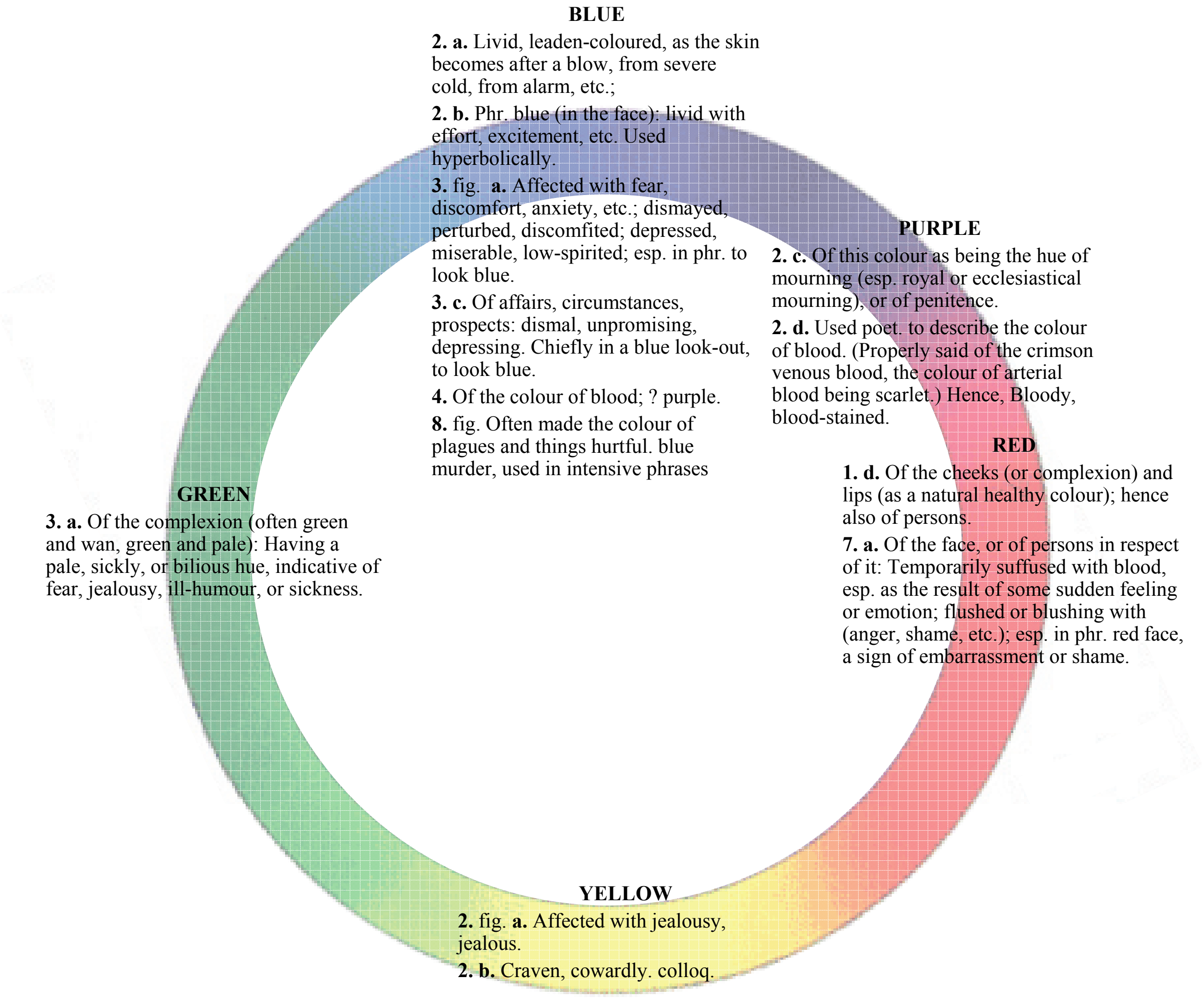
(**a**) Distribution of colors of cartoon smileys that are happy, sad, angry and sick. Data are from two companies that create these cartoon images for use on internet forums: allemoticons.com and smileycentral.com. For the former, 90 happy faces, 83 sad faces, 85 angry faces, and 29 sick faces were obtained. For the latter, 42 happy faces, 22 sad faces, and 25 angry faces were obtained (there were no faces categorized as "sick"). (**b**) The base-line color for these cartoon faces tends to be yellow, and shown here are the distributions for "sad", "angry" and "sick" from (a), but now normalized by the "happy" distribution. One can see that sad faces have a tendency to be colored blue, that angry faces tend to be colored red, and that sick faces tend to be colored green. The moral here is to provide some evidence that color modulations of skin appears to be sufficiently used by people even today that companies can utilize colors around the hue circle to convey emotions.



Supplementary Figure 4, Changizi et al., "…primate color vision…"

Supplementary Figure 5

Entries in the Oxford English Dictionary (Second edition) for color terms that relate to emotion, skin or blood. Note that because the two variables that affect skin color are blood-related, color associations to blood are not independent from associations to skin.



BLUE

2. a. Livid, leaden-coloured, as the skin becomes after a blow, from severe cold, from alarm, etc.;

2. b. Phr. blue (in the face): livid with effort, excitement, etc. Used hyperbolically.

3. fig. **a.** Affected with fear, discomfort, anxiety, etc.; dismayed, perturbed, discomfited; depressed, miserable, low-spirited; esp. in phr. to look blue.

3. c. Of affairs, circumstances, prospects: dismal, unpromising, depressing. Chiefly in a blue look-out, to look blue.

4. Of the colour of blood; ? purple.

8. fig. Often made the colour of plagues and things hurtful. blue murder, used in intensive phrases

PURPLE

2. c. Of this colour as being the hue of mourning (esp. royal or ecclesiastical mourning), or of penitence.

2. d. Used poet. to describe the colour of blood. (Properly said of the crimson venous blood, the colour of arterial blood being scarlet.) Hence, Bloody, blood-stained.

RED

1. d. Of the cheeks (or complexion) and lips (as a natural healthy colour); hence also of persons.

7. a. Of the face, or of persons in respect of it: Temporarily suffused with blood, esp. as the result of some sudden feeling or emotion; flushed or blushing with (anger, shame, etc.); esp. in phr. red face, a sign of embarrassment or shame.

GREEN

3. a. Of the complexion (often green and wan, green and pale): Having a pale, sickly, or bilious hue, indicative of fear, jealousy, ill-humour, or sickness.

YELLOW

2. fig. **a.** Affected with jealousy, jealous.

2. b. Craven, cowardly. colloq.

Supplementary Figure 5, Changizi et al., "…primate color vision…"

Supplementary Figure 6

Plot of logarithm (base 10) of the luminance of skin, and also ratings of "warmth" or "coolness" of the hues (or "light" and "dark" hues). The luminances were measured as L+M, and are computed relative to baseline skin; we used skin reflectances modulated in blood space as shown in Figure 1c of the main paper, and the dot and squares along the x-axis indicate very approximately where in blood space these colors lie. The color names on the bottom correspond roughly to the direction of the color deviation away from baseline skin. The main observation concerning luminance is that, relative to baseline skin, lowering the hemoglobin concentration in the skin tends to increase luminance, and simultaneously moves the hue toward the yellows, whereas increasing the hemoglobin concentration tends to decrease the luminance, and shifts the hues toward the blues. The result is that the luminance peaks around yellow, and falls to a minimum near blue. Hues are, across cultures, often categorized as "warm" and "cool", or, equivalently, "light" and "dark", and these data are from Katra & Wooten [1] and published in Hardin [2], showing observer judgements of the warmth (positive) versus coolness (negative) of the colors. One can see close similarity between the relative luminance of skin and judgments of the warm or light hues, suggesting a conjecture that perhaps "light" (or "warm") and "dark" ("cool") are given these terms because of the typical luminance modulations of skin when skin moves in those hue directions. Our hypothesis may also allow explanations for why some hues are "strong", such as red: perhaps it signals good physiological condition[3,4] because greater oxygen saturation is difficult to maintain if not in good condition.

References

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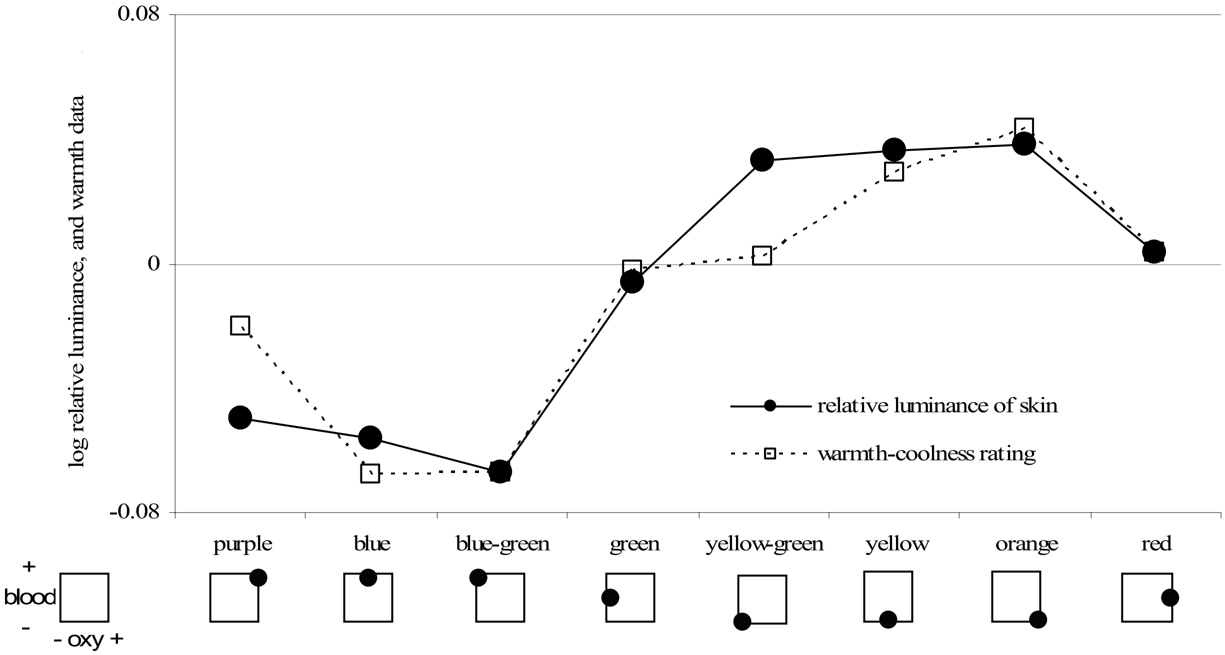

Supplementary Figure 6, Changizi et al., "…primate color vision…"