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Original Article

Attractive Skin Coloration: Harnessing Sexual Selection to Improve Diet and Health

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Abstract: In this paper we review the mechanisms through which carotenoid coloration could provide a sexually selected cue to condition in species with elaborate color vision. Skin carotenoid pigmentation induced by fruit and vegetable consumption may provide a similar cue to health in humans (particularly light-skinned Asians and Caucasians). Evidence demonstrates that carotenoid-based skin coloration enhances apparent health, and that dietary change can perceptibly impact skin color within weeks. We find that the skin coloration associated with increased fruit and vegetable consumption benefits apparent health to a greater extent than melanin pigmentation. We argue that the benefits to appearance may motivate individuals to improve their diet and that this line of appearance research reveals a potentially powerful strategy for motivating a healthy lifestyle.

Keywords: skin color, fruit and vegetables, carotenoids, dietary intervention, appearance

Introduction

Carotenoid Ornaments as Sexually Selected Cues to Condition

Many vertebrate species exhibit carotenoid-based yellow-red coloration in their skin, beaks, feathers, scales or ornaments (Fox, 1976; Goodwin, 1984). A wealth of observational and experimental data indicates that the extent and intensity of carotenoid pigmentation reflects the bearer's condition, particularly in bird and fish species. For instance, the carotenoid-based yellow breast plumage of great tits (*Parus major*) is duller in parasited birds and brighter in those free of infection (Horak, Ots, Vellau, Spottiswoode, and Møller, 2001). Experimentally, inducing a parasite load in blackbirds (*Turdus merula*) leads to decreases in carotenoid-based bill coloration (Baeta, Faivre, Motreuil, Gaillard, and Moreau, 2008) and similar manipulations reduce the intensity of orange carotenoid spots in male guppies (*Poecilia reticulata*) (Houde and Torio, 1992) and red coloration in male sticklebacks (*Gasterosteus aculeatus*) (Milinski and Bakker, 1990). Removal of parasites via antihelmintic treatment increases the redness and size of carotenoid-based combs in red grouse (*Lagopus lagopus*) (Mougeot et al., 2010). Further, male greenfinches (*Carduelis chloris*) with larger carotenoid-based plumage patches are less susceptible to, and exhibit faster clearance of, viral infection (Lindstrom and Lundstrom, 2000).

It follows that preferences for this overt indicator of health may have evolved via sexual selection, as preferentially mating with an extravagantly colored partner is likely to confer direct and indirect fitness benefits to the observer (Hamilton and Zuk, 1982; Hill, 1991). A further body of evidence indeed suggests that perceived mate value is contingent on natural and experimentally induced variation in carotenoid coloration. For example, female guppies preferentially mate with males exhibiting brighter carotenoid-based coloration (Kodric-Brown, 1985). Male house finches (*Carpodacus mexicanas*) with naturally brighter carotenoid plumage were more frequently selected as sexual partners (Hill, 1990) and when the carotenoid coloration of plumage in this species was artificially brightened, males were more likely to find a mate than controls (Hill, 1991).

Carotenoids are efficient scavengers of singlet oxygen species (Sies, 1993), protecting cellular proteins, lipids and DNA from oxidative damage. These pigments are expended in this antioxidant role, and cannot be re-synthesized *in vivo* by animals (McGraw, 2006). Consequently, the systemic level and hence the availability of carotenoids for deposition is widely held to be contingent on a trade-off between their expenditure as antioxidants and display (Lozano, 1994); carotenoid coloration can thereby provide an ‘honest’ cue to the bearer’s condition. Supporting this hypothesis, the experimental administration of a redox-active herbicide (raising oxidative stress) is associated with reduced intensity of carotenoid-based plumage in partridges (*Alectoris rufa*) (Alonso-Alvarez and Galvan, 2011). Also, male sticklebacks with a greater buffer of non-carotenoid antioxidants exhibit more intense carotenoid-based redness (Pike, Blount, Lindstrom, and Metcalfe, 2007).

In line with this hypothesis, carotenoid-based coloration may be a strong indicator of prevailing infection levels due to the nature of primary phagocytic mechanisms. “Respiratory burst” is a process in which pathogens are neutralized by high levels of reactive oxygen species (Babior, Kipnes, and Curnutte, 1973). The non-targeted nature of this defense mechanism necessitates increased expenditure of carotenoids and other antioxidants during periods of infection to mitigate oxidative damage to the host’s tissues. Individuals that regularly experience infections and hence oxidative stress will consequently exhibit reduced levels of circulating carotenoids, which is likely to detract from carotenoid ornamentation (Lozano, 1994).

A further hypothesis proposes that carotenoid coloration may reflect actual condition due to the toxicity of carotenoid breakdown products (Vinkler and Albrecht, 2010). The carotenoid maintenance handicap hypothesis postulates that the toxic by-products of carotenoid oxidation are more likely to be formed when systemic antioxidant reserves are low (Vinkler and Albrecht, 2010). This theory also postulates that the relationship between oxidative stress and carotenoid pigmentation is linked to testosterone, which increases carotenoid bioavailability (Blas, Perez-Rodriguez, Bortolotti, Vinuela, and Marchant, 2006), but simultaneously increases oxidative stress (Wikelski, Lynn, Breuner, Wingfield, and Kenagy, 1999). The honesty of carotenoid ornamentation is preserved as only the individuals with competent antioxidant systems may exhibit intense carotenoid coloration; the oxidation challenge posed by testosterone cannot be endured by individuals with inadequate antioxidant resources (Vinkler and Albrecht, 2010).

A number of endogenous and exogenous factors could, in principle, affect the quantity and quality of antioxidant reserves which, through either of the mechanisms proposed above, may contribute to carotenoid coloration being a reliable cue of condition (e.g., heritable enzymic antioxidant capacity, Cheng, Aggrey, Nichols, Garnett, and Godin, 1997). Dietary quality (as a function of foraging competence or an ability to maintain a food-bearing territory) is likely to be a key determinant of apparent condition in this respect, as carotenoids and a number of additional, colorless, antioxidant phytochemicals are largely or exclusively obtained through consumption of food items containing these important molecules (Rietjens et al., 2002; Smith, Ungnade, and Prichard, 1938). This suggestion is supported by observations that carotenoid coloration is contingent on the abundance of carotenoid-rich food items in the individual’s habitat (Horak et al., 2001; Slagsvold and Lifjeld, 1985) and studies which link experimentally manipulated consumption of carotenoids and non-pigmented antioxidants with plumage, integument and beak coloration (e.g., Bertrand, Faivre, and Sorci, 2006; Hill, 1992, 1993; Jouventin, McGraw, Morel, and Celerier, 2007; Kodric-Brown, 1989; Pike, et al., 2007).

Carotenoids and Human Skin Color

Carotenoid pigments are present in all layers of human skin (Lademann, Meinke, Sterry, and Darvin, 2011) and as in some animal species these pigments, alongside melanin and hemoglobin, impart coloration to human integument, predominantly contributing to normal skin yellowness (Alaluf, Heinrich, Stahl, Tronnier, and Wiseman, 2002). The abundance of carotenoids in the skin is contingent on dietary intake of carotenoid and antioxidant-rich foods. Fruit and vegetable consumption in particular is associated with dermal carotenoid concentrations, as measured *in vivo* via Raman spectroscopy (Darvin et al., 2008; Rerksuppaphol and Rerksuppaphol, 2006) and in biopsy samples via high-performance liquid chromatography (Mayne et al., 2010). Consequently, skin color is partially contingent on diet; across individuals, daily intake of fruit and vegetables is correlated with skin yellowness (Stephen, Coetzee, and Perrett, 2011). Within-person changes in fruit and vegetable consumption are also associated with skin yellowness and redness changes over a six-week period (Whitehead, Re, Xiao, Ozakinci, and Perrett, 2012c).

Carotenoid pigmentation of human skin is perceived as healthy and has recently been suggested to be a more important cue of condition for attractiveness than commonly investigated facial morphology cues (e.g., masculinity, Scott, Pound, Stephen, Clark, and Penton-Voak, 2010; Stephen et al., 2012). When observers are able to manipulate facial skin coloration along a yellowness axis, images are reliably increased in yellowness to optimize apparent healthiness. This holds across black South African, Asian and Caucasian facial stimuli for observers of each of these ethnicities (Stephen, et al., 2011; Stephen, et al., 2012; Stephen, Smith, Stirrat, and Perrett, 2009; Whitehead, Coetzee, Ozakinci, and Perrett, 2012a), suggesting that this cue of health generalizes across cultures.

Similar results are found when participants are asked to manipulate facial skin color along empirically-derived carotenoid pigment and diet-linked color axes. For instance, Stephen et al. (2011) supplemented participants' diets with β-carotene and quantified the impact on skin lightness, redness and yellowness. Observers chose to increase the level of β-carotene pigment coloration (predominantly yellowness) in facial skin to optimize healthy appearance. Participants also preferred β-carotene skin coloration to melanin coloration when these pigments were simultaneously able to be manipulated. Further, in a psychophysical study, observers were able to detect skin color differences associated with modest increases in fruit and vegetable consumption (two portions per day, Whitehead et al., 2012c) suggesting that humans are sensitive at discriminating subtle differences in skin carotenoid pigmentation. These studies have also found that diet-related changes in the spectral reflectance of skin occur selectively at wavelengths associated with peak absorption of light energy by carotenoids (Stephen, et al., 2011). Hence carotenoids, rather than melanin are presumed to be responsible for dietary effects on skin color (Stamatas, Zmudzka, Kollias, and Beer, 2004).

Appearance-Based Dietary Intervention

The research reviewed above suggests that human perception of healthy skin coloration may be used to tackle unhealthy diet in modern society. Inadequate intake of fruit and vegetables is a major cause of preventable illnesses, precipitating incidences of cardiovascular disorder (Bazzano et al., 2002), stroke (Joshipura et al., 1999), diabetes (Harding et al., 2008) and potentially some cancers (Riboli and Norat, 2003, though see Boffetta et al., 2010). Such lifestyle-attributable diseases contribute to over 40% of deaths per year worldwide (WHO, 2003) and 16% of disability-adjusted life-years lost worldwide (WHO, 2003), making it clear that effective behavioral interventions are required in this area. To date, population-level diet campaigns have largely focused on health-based messages, which for instance recommend that individuals consume fruit and vegetables to guard against chronic diseases (e.g.,WHO, 1990). Two decades after the inception of these campaigns, diet remains a key determinant of preventable morbidity and mortality (WHO, 2011), suggesting that it is necessary to investigate alternate methods.

The dietary effects on skin appearance discussed above may provide an additional incentive to improve diet as individuals are strongly motivated to improve their own appearance (Whitehead, Ozakinci, Stephen, and Perrett, 2012b). This drive to optimize attractiveness can be seen as a reflection of the sexual selection pressures facing reproductively aged individuals, which may generalize across the lifespan (Harris and Carr, 2001). Interventions appealing to attractiveness have already proved effective. For instance, young adults showed greater modification of attitudes towards sun-tanning when the negative consequences of UV exposure for appearance were highlighted, compared to warnings about the health implications of this behavior (Jones and Leary, 1994). Further appearance-based interventions in this area have highlighted graphically the impact of UV exposure on participants' own facial appearance. Implementing these techniques has resulted in long-term changes in sun-tanning behavior (e.g., Stock et al., 2009).

Implementation

The impact of fruit and vegetable consumption on skin color could be utilized in a similar way to promote healthy eating. The empirical studies outlined above allow quantification of the impact that carotenoid pigmentation has on skin color. Coupled with this, existing image manipulation techniques (e.g., Burt and Perrett, 1995; Stephen et al., 2009) can be used to transform images of participants' own faces along a skin color axis to accurately illustrate varying degrees of fruit and vegetable consumption (Figure 1). We propose that individuals could view manipulated images of their facial photograph alongside existing effective dietary intervention techniques such as setting dietary goals and self-monitoring progress (see Pomerleau, Lock, Knai, and Mckee, 2005).

It is important to highlight the results of psychophysical studies to intervention participants. Individuals may be more strongly motivated to increase their fruit and vegetable consumption if it is made clear that even modest dietary change is sufficient to confer perceptible skin color benefits (e.g., Whitehead et al., 2012c). It is also important that participants recognize the rapidity of the impact on skin color (Whitehead et al., 2012c) as existing dietary interventions typically concentrate on long-term benefits to health and overlook shorter-term incentives.

Required Research

There are significant gaps in the evidence that would accompany a public health intervention of this type. It is important that participants are motivated to increase their fruit and vegetable consumption, rather than opt for a course of β-carotene supplementation, as fruit and vegetable consumption confers health benefits beyond those associated with dietary supplementation. Fruit and vegetables are rich in other beneficial antioxidants and nutrients, including many additional carotenoids, flavenoids, polyphenols, vitamins and selenium (Pennington and Fisher, 2010). Supplements ingested in tablet or capsule form are also unable to provide sufficient levels of dietary fiber, which is important for gastrointestinal health (Eastwood and Kritchevsky, 2005). Further, people tend to eat a relatively consistent weight of food each day (WHO, 2005), thus a diet that includes a greater proportion of fruit and vegetables will reduce the consumption of foods high in energy and saturated fats which themselves are associated with disorders such as cardiovascular diseases and hypertension (Johnson et al., 2009). β-carotene supplementation may also be harmful in high doses (Tanvetyanon and Bepler, 2008). Carotenoids have diverse absorption spectra and will therefore affect skin color in subtly different ways. The research reviewed above suggests that a range of the 600-plus carotenoid pigments could confer benefits to the observer via sexual selection.

The perception of skin coloration induced by fruit and vegetable consumption has yet to be compared with melanin pigmentation. Many Caucasian individuals actively seek melanization via ultraviolet light exposure with the aim of improving appearance (Jones and Leary, 1994). An appearance-based dietary intervention such as that outlined above may be additionally useful in reducing the prevalence of this dominant cause of skin cancer (Armstrong and Kricker, 2001). This approach may be particularly effective if dietary impacts on skin color are equivalent to, or perceived as healthier than the impact of melanization. We investigate this possibility in the brief perceptual study below by enabling participants to simultaneously manipulate skin color along separate melanin and fruit and vegetable consumption skin color axes, in order to optimize the appearance of healthiness.

Table 1. Maximum and minimum spectrophotometer-derived transformation values along each empirically derived pigment axis in CIE L*a*b* color space

		ΔL*	**Δa***	**Δb***	***ΔE***
Melanin	+	-10.4	-2.42	14.2	17.8
	-	10.4	2.42	-14.2	
Fruit and vegetable consumption	+	-4.12	5.16	15.96	17.2
	-	4.12	-5.16	-15.96	

Note: L* reflects degrees of lightness and positive values of a* and b* reflect degrees of redness and yellowness, respectively. Each pigment continuum comprised 21 images, representing equal steps within these L*a*b* value ranges. The centre image of each continuum represented no change from the original photograph. *ΔE* is a standard way of representing color differences in CIE L*a*b* space and here represents the maximum and minimum color change applied to original photographs. Fruit and vegetable consumption color-value ranges represent increased and decreased consumption of between +40 and -40 portions per day over a six week period, respectively. These values were purposefully chosen to represent an extreme range

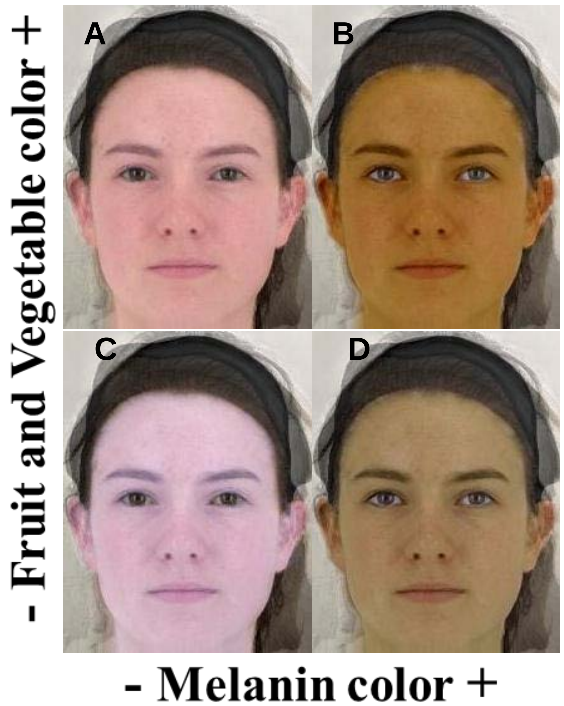
Materials and Methods

All procedures were subject to ethical approval from the University of St Andrews Teaching and Research Ethics Committee.

We used existing spectrophotometer measurements to define the impact of melanin and fruit and vegetable consumption on human skin color (in CIE L*a*b* color space, where L* reflects degrees of lightness and positive values of a* and b* reflect degrees of redness and yellowness, respectively). Melanin pigmentation was determined by measuring the difference between a sun-exposed outer arm skin region and an occluded shoulder region. (Table 1, Stephen et al., 2011). The impact of fruit and vegetable consumption on skin color was determined by measuring mean change in facial skin color per portion change in fruit and vegetable consumption (Table 1, Whitehead, unpublished data).

Color-calibrated facial photographs were taken of 30 Caucasian participants (15 female, 15 male, mean age 20.5, see Whitehead et al., 2012c for methods). The skin portions of these images were transformed according to the empirically derived pigment color ranges in Table 1 (see Stephen et al., 2009 for methods). Initially, faces were transformed according to the impact that fruit and vegetable consumption has on skin color.

Figure 1. Coloration applied to faces along a melanin skin color axis and fruit and vegetable skin color axis



Note: Images A and C reflect low melanin coloration, images B and D reflect high melanin coloration. Images A and B additively reflect high fruit and vegetable coloration, images C and D reflect low fruit and vegetable coloration. Images represent ± 50% transforms, see Table 1 for maximum pigment color transform values.

A continuum of 21 images was created for each of the 30 identities. Skin portions of face images were transformed in 21 equal steps across the continuum and lightness, redness and yellowness were manipulated simultaneously. Each continuum was organized such that the endpoints represented the maximal color changes and the center image of each set represented no color change from the original photograph.

Per identity, each of the resulting 21 images in the fruit and vegetable skin color continuum were then similarly transformed along the melanin color axis. This resulted in a 21x21 matrix of 441 images for each of the 30 identities. These matrices contained independent skin color manipulations associated with fruit and vegetable consumption and melanin pigmentation (see Figure 1).

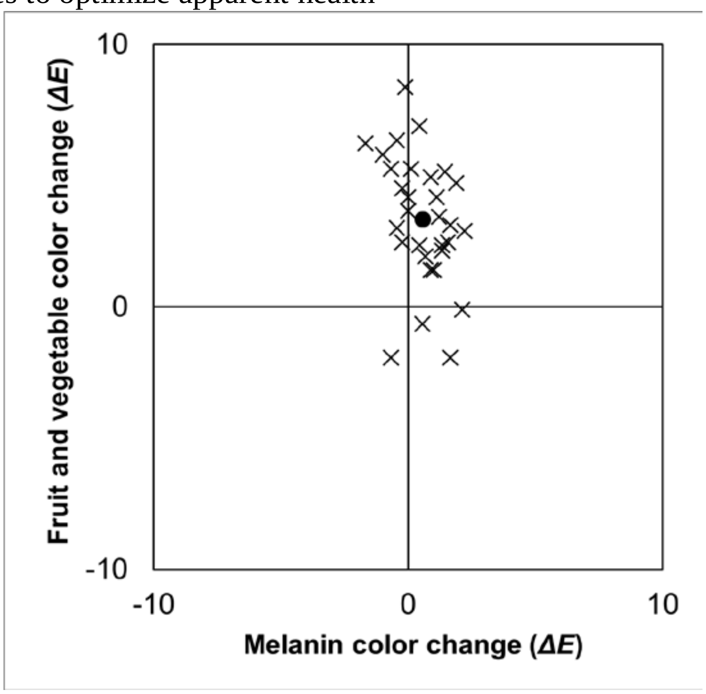
A computer program controlled matrix display. At any one time, only one face image was visible. Participants selected, via horizontal movements of a mouse cursor, the position along one pigment axis. Simultaneously, vertical movements of the cursor allowed independent selection along a second pigment axis. Direction of movement, axis center location and axis arrangement were randomized to prevent learning effects. All 30 image matrices were sequentially presented to a separate group of 16 Caucasian participants (13 female, 3 male, mean age 24.6) asked to “Make the face look as healthy as possible”. Participants viewed stimuli on a color-calibrated monitor in a darkened booth. The computer program stored participants’ chosen position on each of the pigment axes and advanced to the next randomly selected matrix.

Results

When participants were able to manipulate the level of melanin skin coloration as well as the fruit and vegetable skin consumption color axis, we saw significant increases in pigmentation along both continua (melanin: $t(29) = 3.15$, $p = 0.004$, fruit and vegetable coloration: $t(29) = 7.37$, $p < 0.001$, approximately associated with an increased consumption of 7.75 portions per day, see Figure 2). Twenty-six of 30 faces benefited from increases in skin coloration associated with fruit and vegetable consumption and 21 of 30 benefited from increased melanin coloration.

In order to optimize apparent health, participants added significantly less melanin coloration than fruit and vegetable associated skin coloration ($t(29) = 5.07$, $p < 0.001$). Participant manipulation of images along both continua conferred an average additive skin color change of 3.70 ΔE (-0.46 L*, +0.92 a* and +3.55 b* units change applied to the original images).

Figure 2. Color change applied (ΔE, a standard way of representing color differences in CIE L*a*b* space) along a melanin skin color axis and a fruit and vegetable skin color axis to original face images to optimize apparent health



Note: Crosses represent individual faces (responses across all participants) and the filled circle represents mean chosen position across all faces.

Discussion

In line with previous research (Stephen et al., 2009, 2011; Whitehead et al., 2012c), this study demonstrates that the skin coloration associated with increased dietary consumption of fruit and vegetables is perceived as healthy. Previous research finds that β-carotene pigmentation is perceived as healthier than melanization (Stephen et al., 2011). Our research suggests that this generalizes to dietary consumption of many carotenoids, as we find that skin color associated with fruit and vegetable consumption influences apparent health to a greater extent than melanin pigmentation

Conclusions and Future Directions

The study conducted here further suggests that human perception of diet-linked changes in skin color could be used to shape a dietary intervention strategy. As elsewhere in the animal kingdom, human skin coloration reflects dietary consumption of carotenoids in a manner that improves apparent condition. Future appearance-based interventions can advise increased consumption of a wide variety of fruit and vegetables, rather than β-carotene supplements, ensuring the maximum health benefit.

Diet-linked skin coloration has a larger impact on apparent health than melanization. Therefore, we also conclude that advertising the results of the present study could be persuasive in motivating individuals to eschew the dangers of excess UV exposure in favor of improving diet, which we show to be a more effective way of improving appearance. To test the implications of our work, it is necessary to conduct randomized, controlled trials across a range of demographic factors (e.g., age, ethnicity, gender, socioeconomic status) to determine the long-term impact of appearance-based intervention on behavior and health.

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