

Hair Color Measurement and Variation

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ABSTRACT Pigmentation of hair in humans has been investigated by medical scientists, anthropologists and, more recently, by forensic scientists. In every investigation, hair color must first be defined by the researchers. Subjective color assessment inhibits the reproducibility of experiments and the direct comparison of results. The aim of this study was to objectively measure human hair color and examine the variation found in a population with European ancestry, using the CIE L*a*b* color space. Observer-perceived hair colors were compared with self-reported hair colors and the color as measured by reflective spectrophotometry of 132 subjects of European ancestry. The presented data show that self-reported hair

colors and observer-reported colors are similar; however, these categories are not necessarily the best way to categorize hair color for quantitative research. Using a two-step cluster analysis, hair color can be divided into categories or clusters based on spectrophotometric measurements in the CIE L*a*b* color space and these clusters can be well discriminated from each other. This separation is primarily based on the b* (yellow) color component and the clusters show agreement to observer-reported colors. This study illustrates the possibilities for and necessity of objectively defining the hair color phenotype for various downstream applications. *Am J Phys Anthropol* 137:91–96, 2008. © 2008 Wiley-Liss, Inc.

Human pigmentation has been observed and studied for over 4000 years (Westerhof, 2006) and is an integral part of our physical health and cultural identity. Normal pigmentation variation in humans has been investigated by medical scientists (Duffy et al., 2004), anthropologists (Parra et al., 2004; Parra, 2007) and, more recently, by forensic science researchers for the prediction of physical characteristics from DNA, to be used as an investigative tool. The prediction of physical traits for use in forensic investigations is a developing field and hair color is one of many traits that may assist investigators in limiting a suspect pool. The UK Forensic Science Service has already implemented a test with 84% accuracy for predicting red hair (Grimes et al., 2001).

Hair color has received somewhat less attention in the study of pigmentation than skin or eye color, with most work on hair color being done as a consequence of, or in conjunction with, other pigmentary traits (such as skin color or melanoma risk) (Sturm et al., 2003; Duffy et al., 2004). These investigations have led to a great deal of information on red hair (Box et al., 1997; Grimes et al., 2001; Ha et al., 2003; Sturm et al., 2003; Duffy et al., 2004; Naysmith et al., 2004), which is associated with skin cancer risk; however data on non-red hair colors is scarce. Researchers contributing to the scientific investigation of hair color represent the different fields of medical science and genetics (Ancans et al., 2003; Ha et al., 2003; Duffy et al., 2004), the cosmetics industry (Takahashi and Nakamura, 2004, 2005), and forensic science (Grimes et al., 2001), as well as the disciplines of chemistry and toxicology (Borges et al., 2001; Nogueira and Joeke, 2004). There has also been interest in the hair color of our hominid relatives; a recent study has determined that Neanderthals had variants in a gene that is associated with differing pigmentation levels in *Homo sapiens* (Lalueza-Fox et al., 2007).

The extinct Neanderthals were a hominid species that lived in Europe and western Asia (Krause et al., 2007).

Modern *Homo sapiens* from the same geographical area show almost all of the hair color variation found in human populations. From studies of genetic sequence diversity (Harding et al., 2000), it has been concluded that there was positive selection pressure for maintaining dark skin and hair pigmentation in the southern latitudes of Africa and Asia, where it protected an individual from ultraviolet light from the sun (Rees, 2003; Parra, 2007). When human populations migrated to more northern latitudes, there was less pressure to maintain dark pigmentation and instead, light skin pigmentation became a selective advantage (e.g., through the easier synthesis of Vitamin D) (Rees, 2003; Parra, 2007). The possibility of sexual selection being a factor in the evolution of pigmentation variation is supported by the presence of sexual dimorphism in skin pigmentation and by evidence suggesting that pigmentation influences mate selection (Aoki, 2002; Madrigal and Kelly, 2007a; Parra, 2007); however, difficulties arise in trying to isolate and quantify the effects of natural and sexual selection (Frost, 2007; Madrigal and Kelly, 2007a,b).

Evidence suggests that hair and skin color are somewhat correlated, within the European population (Shriver and Parra, 2000), and hair color is likely the result of similar selective pressures; however, the exact genetic mechanisms of hair color and its high variability, as well as other factors in the biology of hair color have not yet been fully elucidated.

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In every investigation, "hair color" must first be defined by the researchers. What one investigation calls "blonde" however, might be what another calls "light brown" and this inhibits the reproducibility of experiments and the direct comparison of results.

Reflective spectrophotometry has been used to objectively measure skin pigmentation (Shriver and Parra, 2000; Parra et al., 2004) and the technique has also been used on hair in different ways and for various purposes including cosmetic science (Takahashi and Nakamura, 2004, 2005), for the determination of hair composition and structure (Nogueira and Joeke, 2004), for comparison of measurement methods (Shriver and Parra, 2000), and in recent genetic studies (Naysmith et al., 2004). It has been found to be an objective and effective way to measure hair color.

To objectively measure hair color presupposes a method of color measurement. There are, however, numerous models or "color spaces" used to describe color. The model developed by the Commission Internationale de l'Eclairage, CIELAB or CIE $L^*a^*b^*$, measures color on three axes that are nearly linear with human perception (Ford and Roberts, 1998). This model provides a grid point for each specific color (TASI, 2004) and in addition, has been used for other studies of human pigmentation (Shriver and Parra, 2000; Takahashi and Nakamura, 2004, 2005; Parra, 2007).

In the CIE $L^*a^*b^*$ color space, the lightness, or intensity, of a color is measured on the " L^* " axis on a scale from 0 (black) to 100 (white). The color is then measured on the " a^* " axis which gives a value from -100 (green) to +100 (red). The " b^* " axis measures color from -100 (blue) to +100 (yellow). One unit on the L^* , a^* , or b^* axes is considered to be the smallest difference the human eye can detect (TASI, 2004). This color grid point allows for the mathematical comparison of color. It should be noted that, theoretically, the a and b axes have no maximum or minimum values but this research has used the cut off points of ± 100 because these represent the practical limit of the instrument used in the color measurement (Napier S, personal communication, Biolab Group, Australia, 2007).

In 2000, Shriver and Parra used the CIE $L^*a^*b^*$ system with reflective spectrophotometry to measure the hair color of 41 European-American individuals and 18 individuals of non-European ancestry, comparing the L^* color component to the Melanin Index. They found a significant correlation between these systems of measurement and reported low variability in the hair color of individuals of non-European ancestry. Naysmith et al. in 2004 used the CIE $L^*a^*b^*$ system to measure the hair color of 50 individuals for genetic and chemical studies of red hair. They found relationships between variations in the gene MC1R and measured hair color (most strongly with b^*), as well as with chemical studies. It should be noted that people with red hair were deliberately over-represented in this sample and volunteers ranged in age from 6 to 72 years old (median of 35). Both studies emphasized the necessity and demonstrated the feasibility of measuring pigmentation objectively and accurately.

The aim of the research presented here was to objectively measure human hair color and examine the variation found in a population with European ancestry, over all three color axes. Young adult volunteers were recruited due to the fact that hair color is known to change with age and especially during puberty and late

adulthood (Slominski et al., 2004). We were particularly interested in the variation found among the non-red colors (i.e., blonde, brown, and black). Observer-perceived hair colors were compared with self-reported hair colors and the color as measured by reflective spectrophotometry. The variation of the measured hair colors was then analyzed to determine if and how hair colors form describable groups and how these match with our intuitive descriptions of hair color.

Objectively describing categories of hair color will benefit the fields of anthropology and medical science and may introduce some standardization into the design of genetic studies. It could also benefit forensic investigation on various levels, for example, specific criteria may help in better communication between witnesses, investigators, and forensic hair-examiners and be an important part in the future of forensic phenotype-profiling and prediction of physical features from DNA samples.

MATERIALS AND METHODS

Subjects

Subject recruitment and sampling procedures were conducted with the approval of the Victoria University Human Research Ethics Committee. In total, 140 subjects were included in this analysis. All volunteers recruited for the study had their natural hair color at the time of sampling. Most volunteers were between the ages of 18 and 35 and were of European ancestry (132 subjects). The exceptions to these criteria include six individuals of non-European ancestry (one African and five South Asians) and two older European individuals with white hair. Subjects fitting these criteria were chosen to meet the study aims of examining natural variation in adult European hair color, with non-European and mature-white haired individuals included for comparison purposes.

Sampling

Subjects were first given all project information and the following procedures carried out following their written consent (in compliance with Victoria University Human Research and Ethics standards; approval number HRETH06/156). Subjects filled out a questionnaire that, in addition to confirming their age, ancestry, and natural hair color status, asked them to report how they saw their own hair and eye color. Hair color was reported to be one of; Black, Dark Brown, Light Brown, Blonde, or Red. Color assessment by an observer (the researcher taking the samples) was also recorded.

Hair color was measured by reflective spectrophotometry (RS) using a Minolta CR-300 Chroma Meter (Konica Minolta, North Ryde NSW, Australia). The instrument was calibrated using a white tile and a light source input setting of "D65" which represents daylight without spectral highlights. The instrument was set to measure in the CIE $L^*a^*b^*$ format. Hair color was measured on the left, right, and back of the head and was measured five times at each spot, the mean of the 15 measurements being the focus of subsequent statistical considerations. The standard deviation of the 15 measurements for each individual ranged from 0.07 to 4.67 for L^* , 0.01 to 2.51 for a^* , and 0.03 to 3.3 for b^* with means of 1.22, 0.33, and 0.68, respectively.

TABLE 1. The self-reported hair colors (SRC) compared to the observer-reported hair colors (ORC)

Color	Self reported	Observer reported
Black	8	12
Dark Brown	52	44
Light Brown	37	44
Blonde	33	31
Red	8	7
White	8	12

Statistics

SPSS 15.0 for Windows (©SPSS Inc. 2006, Chicago IL) was used to analyze the color data. Two separate methods were used—a cluster analysis and discriminant analysis. Measured hair color (by RS) was broken into several groups using a two-step cluster analysis; performed using the Euclidian distance criterion or the log-likelihood probability approach and either not specifying the number of clusters to be formed or asking for a specific number of clusters, ranging from two to seven. Cluster analysis seeks to identify natural subgroups within a population by minimizing within-group variation while maximizing between-group variation. To characterize and evaluate the clusters a separate, discriminant analysis was then performed. Discriminant analysis commences from the perspective of there being a known number of population subgroups. From the population, there are a number of individuals whose subgroup classification is known. The data from these individuals is analyzed in an attempt to build a profile of subgroup membership and subsequently use this profile to classify new individuals (whose subgroup membership is otherwise unknown).

After the analysis, SPSS determines which variables are most important in discriminating the groups, and how good this model will be at predicting group membership of future individuals. It determines the predictive value of the model by removing each individual separately, reanalyzing the data, and then predicting the membership of that case. The percent correctly classified is reported.

RESULTS

Reported colors

Self-reported hair colors (SRC) were compared to the colors determined by the observer (observer-reported color or ORC) (Table 1). 85.7% of individuals had the same hair color reported by themselves and the observer. Where there was a difference, discrepancies were lighter or darker by one shade. The observer was more likely (55% of disagreeing observations) to see a darker shade. The observer classified four SRC Dark Browns as Black, four SRC Light Browns as Dark Browns, and three SRC Blondes as Light Brown. The observer also classified eight SRC Dark Browns as Light Browns. In one case, a self-reported Red color was reported as Blonde by the observer.

Population variation

To examine the hair color variation amongst the European population, the L^* , a^* , and b^* values of the 134 European individuals, as measured by reflective spectro-

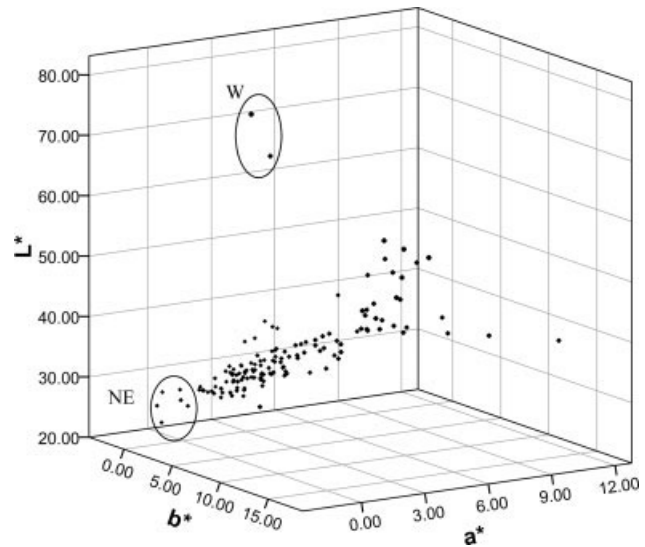


Fig. 1. Population Sample; the non-European samples (NE) and the mature-white haired samples (W) are highlighted. The scales for the CIE $L^*a^*b^*$ axes are $L^* = 0$ (Black) to 100 (White), $a^* = -100$ (green) to +100 (red), and $b^* = -100$ (blue) to +100 (yellow). Only the relevant portions of these scales are shown.

photometry, were recorded and the data subjected to statistical analysis. The variability observed in the entire sample is illustrated in Figure 1. This distinctiveness of the non-European individuals (NE in Fig. 1) and the individuals with white hair (W in Fig. 1) can be seen in the highlighted areas. Individuals not of European ancestry have hair that is much darker with a^* and b^* values very close to zero.

Grouping the population

The aim of the statistical analysis was to investigate the major components of the color variation and to see whether hair color falls into groups that would be meaningful for further research. What qualifies as a meaningful group is subjective and may depend on the intended use of the data; however in this case, meaningful groups would be those that separate colors into several distinct groups. For practical purposes, it would also be useful to have groupings that correspond well to colors people already use to report hair color (e.g. Blonde).

The European sample was broken into groups using the two-step cluster analysis. The analysis was first conducted without specifying the number of clusters, using either the Euclidian distance approach or the log-likelihood probability approach. Next, the numbers of clusters were specified, from two to seven for both approaches and a discriminant analysis was then performed. Using the clusters determined as a definitive population subgroup, the percentage of cases correctly classified was used to evaluate the clusters.

The percentage of cases correctly classified in the discriminant analysis for the various methods of cluster determination is shown in Figure 2. When the observer-reported color (ORC) groupings are used, only 73.1% of cases are correctly classified. All other clusters have greater than 95% of cases correctly classified.

Determined automatically, without specifying the number of clusters, the Euclidian distance approach

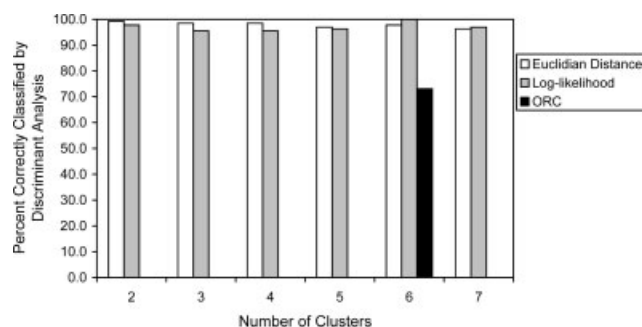


Fig. 2. Discriminant scores for each number of clusters and the method by which they were determined.

TABLE 2. Cluster distribution and characteristics for two clusters determined automatically by the log-likelihood approach (Analysis 1)

	N	% Of Total	L*		a*		b*	
			Mean	SD	Mean	SD	Mean	SD
Cluster 1	35	26.1%	47.05	8.95	4.55	1.88	10.78	2.45
Cluster 2	99	73.9%	32.15	3.08	2.16	0.90	2.99	2.05
Total	134	100%						

yielded no useful clusters, while the log-likelihood method grouped the population into two clusters, the composition of which are shown in Table 2 as an example of how clusters are described. When using the Euclidian distance to determine clusters, having two or three clusters results in very poor sample composition, with more than 97% and 93.3% of cases, respectively, in one cluster. From the remaining groups, two and six clusters as determined by the log-likelihood approach (which will be referred to as Analysis 1 and 2, respectively), and four clusters as determined by the Euclidian distance approach (which will be referred to as Analysis 3) showed the highest discriminant scores and the best group composition (data not shown).

During analysis, canonical discriminant functions are determined. These unstandardized functions are used to make classifications in the discriminant analysis and the standardized function coefficients are used to compare the relative importance of each function and each variable in making classifications. The coefficients of the standardized functions shown in Table 3 show that the most informative function in all three analyses is most highly correlated with the b^* component of color (yellowness) and where there is more than one function, the second most important function is most highly correlated with L^* (lightness). In Analyses 2 and 3, the third discriminant function contributed 1% and 0.9% of information, respectively (data not shown).

An example on the use of the unstandardized functions is shown in Figure 3, which illustrates the use of the function in discriminating between the two clusters determined in Analysis 1 ($F = -5.615 + 0.102L^* + 0.212a^* + 0.270b^*$). Using this function, 97.8% of new cases are correctly classified and this clear distinction between the two groups is visible in Figure 3.

Comparing clusters to the observer-reported colors

It appears that the clusters determined by various methods do show similarity to hair colors as perceived

TABLE 3. Coefficients of the standardized discriminant functions for the three discriminant analyses

Analysis function	1	2		3	
	1	1	2	1	2
L^*	0.535	0.214	0.988	-0.506	1.230
a^*	0.261	0.586	-0.613	-0.612	-0.405
b^*	0.585	0.754	-0.294	0.945	-0.228
	100%	76.3%	22.6%	57.0%	42.1%

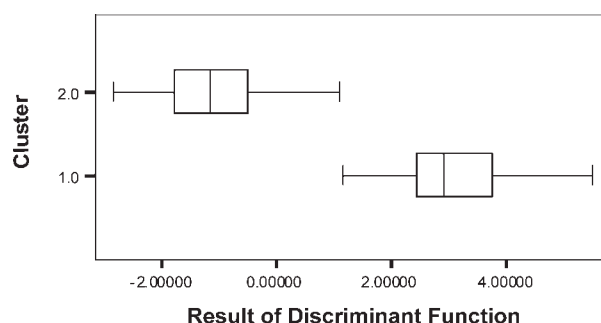


Fig. 3. The results of applying the discriminant function on the $L^*a^*b^*$ data, divided by cluster for the two clusters determined by the log-likelihood method (Analysis 1).

by an observer. When divided into two clusters by the log-likelihood approach (Analysis 1), the observer-reported hair colors Black, Dark Brown, Light Brown, and the four darkest Blondes are in Cluster 1 and the remaining Blondes and all Reds and Whites are in Cluster 2. This shows that the separation in these clusters determined by their L^* , a^* , and b^* values correspond well to divisions in observer-reported colors and could be referred to as "Dark" and "Fair." The names are arbitrary; however, they correspond to how people tend to refer to hair color.

The six clusters determined by log-likelihood (Analysis 2) separate the ORC White very clearly and the four Reds with the highest a^* value (the most red). The other colors are somewhat less distinct; however, they are roughly divided into categories that could be called "Fair," "Light," "Medium," and "Dark." The example shown in Figure 4 illustrates the separation of the six clusters by applying the two most important discriminant functions (a) and the results of using the same functions on the observer-reported groupings (b), where blurring between the groups can be seen.

When four clusters are determined by the Euclidian Distance approach (Analysis 3), the ORC White is clearly separated, as are the two Reds with the highest a^* and b^* values. The rest of the population is divided into two clusters, the first with the darker colors and the other with the fair colors. It should be noted that the separation of fair from dark hair in these groups is similar to that of the two cluster groupings, with four extreme individuals (very light and yellow and the very red) being separated.

DISCUSSION

The presented data show that when given a limited choice of colors, self-reported hair colors and those reported by an observer are fairly consistent; however, these categories are not necessarily the best way to cate-

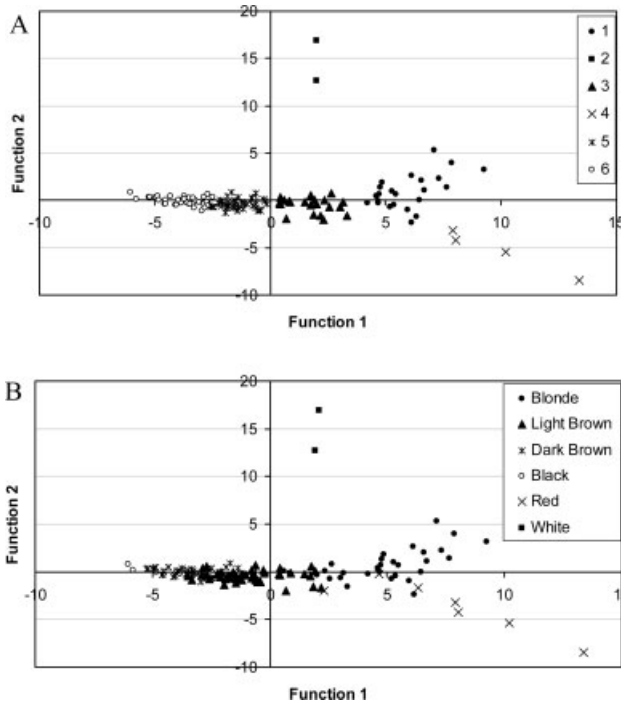


Fig. 4. The first two functions used to discriminate the six clusters as determined by log-likelihood (Analysis 2) were applied to the $L^*a^*b^*$ data and grouped by Cluster (A) and by observer-reported color (B) where $F1 = -0.013 + 0.073L^* + 0.891a^* + 0.573b^*$ and $F2 = -8.477 + 0.338L^* - 0.932a^* - 0.224b^*$.

gorize hair color for quantitative research. Although hair color can be perceived as a continuum (as seen in Fig. 1), it can be divided into categories or clusters based on spectrophotometric measurements in the CIE $L^*a^*b^*$ color space and these clusters can be well discriminated from each other. The discrepancies between self-reported hair color and observer-reported hair color and the poor separation of observer-reported color groups compared to those defined by clustering analysis emphasize the importance for objective measurement of individuals to be included in research studies. For repeatability and validity of studies, phenotypes must be defined as well as possible and the objective measurement methods and analysis strategies presented here may be of assistance in this regard.

The discriminant functions used to make classifications show some interesting results. It can be seen that, when using the CIE $L^*a^*b^*$ color space, the b^* component (yellow) is the most important in describing the variation and grouping of hair colors, followed closely by L^* , in the clusters examined in this study. This suggests that using one component is not sufficient for examining hair colors, as has been done in previous studies (Shriver and Parra, 2000) and that yellow (b^*) is the primary contributor instead of L^* . This, interestingly, corresponds to the 2004 study by Naysmith et al. (2004) where b^* was shown to have the strongest relationship to MC1R genotype. The red component of hair contributes very little information to discriminating groups. The reduction of three color components to one or two discriminant functions makes the examination and classification of individuals easier to represent.

It is also interesting to note that, while not exact, clustered groupings follow the same pattern that self- and observer-reported colors do. How someone decides to report a hair color may be an artifact of the arbitrary naming of colors or of personal bias or it may also be due to human perception of color, which corresponds to the CIE $L^*a^*b^*$ system of measurement. The human eye is a complicated structure with retinal receptors (rods and cones) that are sensitive to changes in lightness and color (Hunt, 1998). Very generally, when receiving a visual signal, these receptors judge the brightness of that signal (mainly the rods) as well as analyzing the hue of a signal as green or red and as blue or yellow (mainly the three types of cones), with this combination of signals being perceived as a color (Hunt, 1998). This system of human trichromatic vision may be why similar groups are defined by both the human reporting of color and by the spectrophotometry and clustering method described here. The lack of sensitivity in biological perception may contribute to the variability found. As mentioned previously, one unit on the $L^*a^*b^*$ scale is defined as the limit of human discrimination between colors (TASI, 2004). The difference between members of different clusters can be less than this in one or more of the three color axes and may contribute to the inconsistency between reported color groups and clusters determined by spectrophotometric data and clustering algorithms.

The particular clustering algorithms and program options used will depend on the intended use of the data. For example, a medical genetic association study may require a Fair/Dark division, where the prediction of hair color in a forensic study may require more specific groupings. This study has illustrated the possibilities by using a two-step cluster analysis in SPSS; however, there are many other programs and clustering algorithms available. Having objectively measured colors allows researchers to group individuals in clearly defined ways and to change these groups as the study demands without subjectivity or collecting additional data.

For practical purposes, it is acknowledged that the exact functions and cluster details may change as larger samples are analyzed and that reflective spectrophotometry, while accurate, may be inconvenient for measurements on very large numbers of people or for investigators and the authors hope to address these issues in the near future.

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LITERATURE CITED

- Ancans J, Flanagan N, Hoogduijn MJ, Thody AJ. 2003. P-locus is a target for the melanogenic effects of MC1R signalling: a possible control point for facultative pigmentation. *Ann NY Acad Sci* 994:373–377.
- Aoki K. 2002. Sexual selection as a cause of human skin colour variation: Darwin's hypothesis revisited. *Ann Hum Biol* 29: 589–608.
- Borges CR, Roberts JC, Wilkins DG, Rollins DE. 2001. Relationship of melanin degradation products to actual melanin content: application to human hair. *Anal Biochem* 290:116–125.
- Box NF, Wyeth JR, O'Gorman LE, Martin NG, Sturm RA. 1997. Characterization of melanocyte stimulating hormone receptor

- variant alleles in twins with red hair. *Hum Mol Genet* 6:1891–1897.
- Duffy DL, Box NF, Chen W, Palmer JS, Montgomery GW, James MR, Hayward NK, Martin NG, Sturm RA. 2004. Interactive effects of MC1R and OCA2 on melanoma risk phenotypes. *Hum Mol Genet* 13:477–461.
- Ford A, Roberts A. 1998. Colour space conversions. www.poynton.com/PDFs/coloureq.pdf
- Frost P. 2007. Human skin-color sexual dimorphism: a test of the sexual selection hypothesis. *Am J Phys Anthropol* 133: 779–780.
- Grimes EA, Noake PJ, Dixon L, Urquhart A. 2001. Sequence polymorphism in the human melanocortin 1 receptor gene as an indicator of the red hair phenotype. *Forensic Sci Int* 122:124–129.
- Ha T, Naysmith L, Waterson K, Oh C, Weller R, Rees JL. 2003. Defining the quantitative contribution of the melanocortin 1 receptor (MC1R) to variation in pigmentary phenotype. *Ann NY Acad Sci* 994:339–347.
- Harding RM, Healy E, Ray AJ, Ellis NS, Flanagan N, Todd C, Dixon C, Sajantila A, Jackson IJ, Birch-Machin MA, Rees JL. 2000. Evidence for variable selective pressures at MC1R. *Am J Hum Genet* 66:1351–1361.
- Hunt RWG. 1998. Measuring colour. Kingston-upon-Thames, 3rd ed. England: Fountain Press. p 19–30.
- Krause J, Orlando L, Serre D, Viola B, Prüfer K, Richards MP, Hublin JJ, Hänni C, Derevianko AP, Pääbo S. 2007. Neanderthals in Central Asia and Siberia. *Nature* 449:902–904.
- Lalueza-Fox C, Rompler H, Caramelli D, Staubert C, Catalano G, Hughes D, Rohland N, Pilli E, Longo L, Condemi S, de la Rasilla M, Fortea J, Rosas A, Stoneking M, Schöneberg T, Bertranpetit J, Hofreiter M. 2007. A melanocortin 1 receptor allele suggests varying pigmentation among Neanderthals. *Science* 318:1453–1455.
- Madrigal L, Kelly W. 2007a. Human skin-color sexual dimorphism: a test of the sexual selection hypothesis. *Am J Phys Anthropol* 132:470–482.
- Madrigal L, Kelly W. 2007b. Human skin-color sexual dimorphism: a test of the sexual selection hypothesis. Reply to Frost (2007). *Am J Phys Anthropol* 133:780–781.
- Naysmith L, Waterson K, Ha T, Flanagan N, Bisset Y, Ray A, Wakamatsu K, Ito S, Rees JL. 2004. Quantitative measures of the effect of the melanocortin 1 receptor on human pigmentary status. *J Invest Dermatol* 122:423–428.
- Nogueira ACS, Joeke I. 2004. Hair color changes and protein damage caused by ultraviolet radiation. *J Photochem Photobiol B* 74:109–117.
- Parra EJ. 2007. Human pigmentation variation: evolution, genetic basis, and implications for public health. *Yearbk Phys Anthropol* 50:85–105.
- Parra EJ, Kittles RA, Shriver MD. 2004. Implications of correlations between skin color and genetic ancestry for biomedical research. *Nat Genet* 36:s54–s60.
- Rees JL. 2003. Genetics of hair and skin color. *Annu Rev Genet* 37:67–90.
- Shriver MD, Parra EJ. 2000. Comparison of narrow-band reflectance spectroscopy and tristimulus colorimetry for measurements of skin and hair color in persons of different biological ancestry. *Am J Phys Anthropol* 112:17–27.
- Slominski A, Tobin DJ, Shibahara S, Wortsman J. 2004. Melanin pigmentation in mammalian skin and its hormonal regulation. *Physiol Rev* 84:1155–1228.
- Sturm RA, Duffy DL, Box NF, Newton RA, Shepherd AG, Chen W, Marks LH, Leonard JH, Martin NG. 2003. Genetic association and cellular function of MC1R variant alleles in human pigmentation. *Ann NY Acad Sci* 994:348–358.
- Takahashi T, Nakamura K. 2004. A study of the photolightening mechanism of blond hair with visible and ultraviolet light. *J Cosmet Sci* 55:291–305.
- Takahashi T, Nakamura K. 2005. A study of the photolightening mechanism of red hair with visible and ultraviolet light: comparison with blond hair. *J Cosmet Sci* 56:47–56.
- TASI. 2004. Colour theory: understanding and modelling colour. Technical Advisory Service for Images. Bristol, UK: University of Bristol.
- Westerhof W. 2006. The discovery of the human melanocyte. *Pigment Cell Res* 19:183–193.