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Eye color predicts but does not directly influence perceived dominance in men

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ABSTRACT

This study focuses on the relationship between eye color, gender, and psychological characteristics perceived from the human face. Photographs of 40 male and 40 female students were rated for perceived dominance and attractiveness. Attractiveness showed no relation with eye color. In contrast, eye color had a significant effect on perceived dominance in males: brown-eyed men were rated as more dominant than men with blue eyes. To control for the effect of eye color, we studied perceived dominance on the same photographs of models after changing the iris color. The eye color had no effect on perceived dominance. This suggests that some other facial features associated with eye color affect the perception of dominance in males. Geometric morphometrics have been applied to reveal features responsible for the differences in facial morphospace of blue-eyed and brown-eyed males.

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1. Introduction

Eyes need not necessarily be regarded only as physiological devices of sight, as organs that receive information from outside the organism. Eyes certainly represent structures that offer information about both present and future behavior, as well as the inner attitude of the bearer. Colloquially, eyes are regarded as windows to the soul (Zebrowitz, 1997). Compared to the eyes of our closest relatives, human eyes are somewhat unusual in both color and shape. Specifically, our eyes have very apparent white sclera, the iris may potentially gain different colors spanning from dark brown to light blue, the overall shape is horizontally prolonged, etc. (Kobayashi & Kohshima, 1997, 2001; Tomasello, Hare, Lehmann, & Call, 2007). Eyes are therefore semantic organs to which different biological meanings may be attributed in different contexts (Kleisner, 2008a, 2008b).

There is some evidence of a relationship between iris color and a variety of other factors. Previous investigations have shown that blue-eyed Caucasian children are more behaviorally inhibited than brown-eyed children (Rosenberg & Kagan, 1987, 1989). Blue iris color also covaries with infant high-reactivity, timidity and shyness (Kagan & Snidman, 2004). Moreover, Coplan, Coleman, and Rubin (1998) suggested that eye color is a marker of social wariness in young children. Interestingly, Bassett and Dabbs (2001) reported a relation between eye color and alcohol consumption. The authors showed that individuals with light eyes

consume significantly more alcohol than dark-eyed individuals. Dark-eyed individuals may be more sensitive to some drugs including alcohol, which may prevent them from hard drinking; conversely, light eyed subjects are more prone to anxiety, so they may compensate for their behavioral inhibition by consuming higher quantities of alcohol (Bassett & Dabbs, 2001). According to Christensen and Sacco, stuttering individuals with blond hair and blue eyes show more severe disfluency of speech than other stutterers (Christensen & Sacco, 1989). Eye color is also suspected for its role as a possible medicinal prognostic factor (Cumming, Mitchell, & Lim, 2000; Regan, Judge, Gragoudas, & Egan, 1999).

In many species, including humans (Havlicek, Roberts, & Flegr, 2005; Reynolds, 1996), dominance associated traits have been suggested as honest signals of male genetic quality ("good genes"). The main problem with using eye color as a useful indicator of dominance or submissiveness is that eye color is usually determined by a few genes with a large effect (Duffy et al., 2007; Kayser et al., 2008; Liu et al., 2009) while dominance is probably determined by many genes with additive and non-additive effects, and also by non-genetic factors. The color of an iris cannot change in response to the dominance of a subject. Therefore, to be a truthful indicator of dominance, iris color should either influence the dominance of a subject (for example due to a pleiotropic effect of the gene which directs eye color), or influence the perception of the observer – e.g. females seeking the "good genes" of dominant partners, should cue off of other physical traits which could change during the life of an individual in response to his/her dominance, and which for some reason usually covaries with brown or blue eye color.

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Here, we searched for an association between iris color (blue or brown) and perceived dominance and attractiveness using photos of male and female university students. We also studied whether it is iris color or rather the presence of other morphological traits associated with blue or brown colored irises that play a role in the rater's judgment. Finally, we used a geometric morphometric approach to detect facial morphological traits associated with eye color that may be responsible for differences in raters' judgments.

2. Methods

2.1. Photographs

We took photographs of 80 students (40 males: mean age = 20.8, range: 19–26; 40 females: mean age = 21.2, range: 19–26) from the Faculty of Science, Charles University in Prague, Czech Republic, using digital camera Nikon D40X. All photos were taken using electronic flash and reflection screen; the subjects were seated in front of a white background. Models were instructed to adopt neutral, non-smiling expressions and to avoid any facial cosmetics and other face decorations. All photographs were cropped so that the eyes of all participants were horizontally at the same height and a standard length of neck was visible. Two of the authors (TK: brown-eyed and KK: blue-eyed) independently judged the photos, selecting individuals with either blue or brown eyes. We avoided the intermediate hues of irises usually designated as green. Eye color that does not correspond to blue or brown occurs only infrequently in the Czech population.

2.2. Rating of photographs

Sixty-two raters (31 females and 31 males), mainly students of faculties other than the Faculty of Science, aged 23.8 years on average (females: mean age = 23.4, range: 19–30; males: mean age = 24.2, range: 19–34), were individually invited to judge the photographs. Every person rated the whole set of 80 photos for dominance (or attractiveness) on a 10 point scale where one corresponds to very submissive (unattractive) and 10 to very dominant (attractive). We used ImageRater 1.1 software for the presentation and judgments of all photographs. Both traits, dominance and attractiveness, were judged by 31 raters: *attractiveness* was rated by 15 males and 16 females aged 24.2 years on average (males – 24.5; females – 23.9); *dominance*: 16 males and 15 females, average age: 23.4 (males – 23.9; females – 22.9). We also controlled for the rater's eye color by including the same number of raters with blue and brown eyes.

Raters saw images on a liquid crystal display computer screen with 1280 × 1024 pixel resolution, and indicated the chosen value by mouse clicks on the discontinuous 10 points scale. No time limits for choice indication were imposed; however, the time taken to rate a particular picture on the scale was usually 1–3 s. The order of the photographs was randomized for each rating session. In cases where a rater knew or was acquainted with a person pictured, she/he was instructed not to rate that picture. The ratings of all photographs evaluated by one rater were converted to Z-scores to eliminate the influence of individual differences between raters, and perceived dominance and attractiveness calculated for each photo as its average Z-score.

2.3. Rating of photographs with changed eye color

In order to find out whether there is any specific effect of eye color on perceived dominance (see Section 3) we used the Adobe Photoshop CS 3 software to change the eye color of all 40 photographs of males. The iris color of originally blue-eyed men was

changed to brown and vice versa. This operation was performed in such a way that only the hue of the iris was changed, while the individually specific structural pattern of the iris remained intact.

The changed photographs were judged for perceived dominance by an additional group of 40 raters (20 males, 20 females) aged 22.5 years on average (males – 22.9; females – 22.0). None of the raters that have judged the original set of photographs were again invited to judge the photos with manipulated iris color. The raters were asked whether they noticed “something unusual” in the photographs presented. No mention was made of the manipulation of eye color. In order to be absolutely sure that iris color manipulation did not affect one group more than the other, we presented the photographs to an independent group of raters (11 females, 12 males) aged 17.4 years on average (males – 17.2; females – 17.6) and let them judge every picture on a 10 point scale where one corresponds to very natural and 10 to very unnatural. The photos were rated under the same conditions and using the same methods as described above for the original set of photographs.

2.4. Statistics

The relation between perceived dominance and attractiveness and eye color was tested by *General Linear Models* (GLM) using a mean Z-score of the trait as the dependent variable and the iris color and sex of the rater as factors: because dominance can be expected to correlate with the age of a subject, we included age of the photographed persons into the GLM as a covariate. Effect size was expressed by partial η^2 . Ratings of each of these categories were analyzed separately for male and female sets of photographs. The differences of mean Z-score of the ratings of each photograph before and after eye color manipulation were calculated and tested separately for blue-eyed and brown-eyed male subjects by one sample *t*-test (H_0 : dominance in original faces – dominance in manipulated faces = 0). The association between changed eye color and perceived naturalness of the manipulated photographs was tested by GLM with a mean Z-score of the trait as the dependent variable and the iris color as factor (the age of the photographed persons were added as covariate).

2.5. Geometric morphometrics

Photographs of 40 males (20 blue-eyed and 20 brown-eyed) were analyzed by geometric morphometric methods (GMM) to investigate the shape differences in faces of blue-eyed and brown-eyed males. The GMM represents a set of analytical methods for the multivariate statistical analysis of Cartesian coordinate data of landmark positions: its theoretical background is well understood and it has been widely used in different biological applications (see e.g. Bookstein, 1991; Dryden & Mardia, 1998; Mitteroecker & Gunz, 2009; Schaefer & Bookstein, 2009; Slice, 2005; Zelditch, Swiderski, Sheets, & Fink, 2004). The main advantage of GMM is that it takes into account information about the spatial relationships among the measured variables that is preserved during analysis and statistical results; this information can thus be later visualized in the form of thin-spline deformation grids.

The 72 landmarks (including 36 semilandmarks) were digitized in tpsDig2 software, ver. 2.14 (Rohlf, 2009a). Landmarks are represented as points that are anatomically (or at least geometrically) homologous while sliding semilandmarks serves to denote curves and outlines. Landmark and semilandmark locations on human faces were adjusted according to definitions in Schaefer et al. (2006) and Fink et al. (2005); see Fig. 1. All configurations of landmarks and semilandmarks were superimposed using the generalized Procrustes analysis (GPA), implemented in tpsRelw, ver.

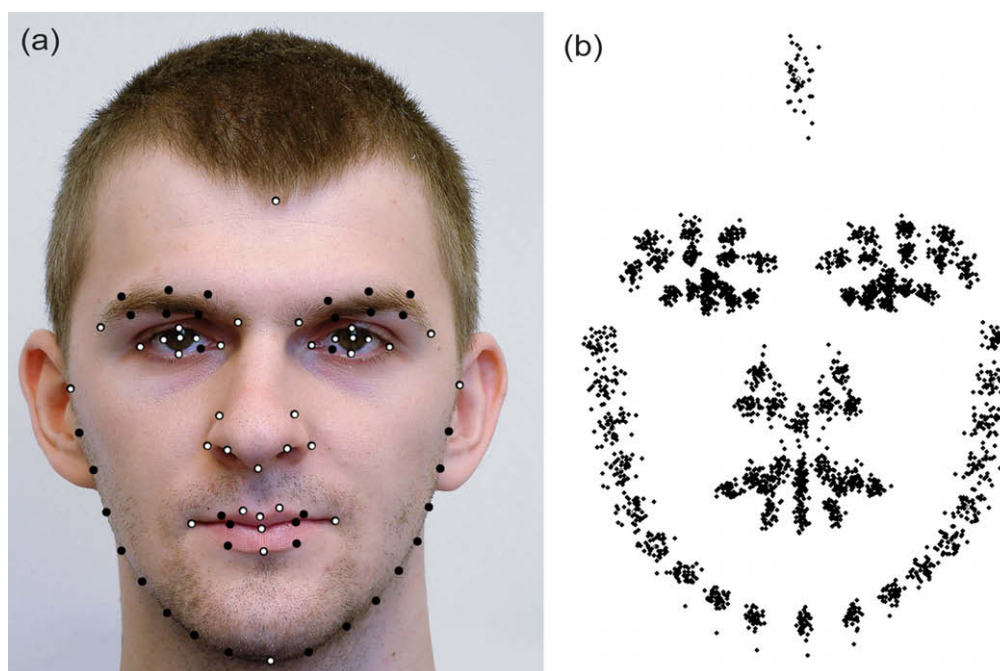


Fig. 1. (a) Configuration of 72 landmark locations on the face: landmarks that can be delimited as anatomically corresponding points – empty circles; semilandmarks that denote curves – filled circles and (b) the superposition of all 72 landmarks for 40 specimens (all males) after the Procrustes fit showing the shape variability in the sample. These data are used for all subsequent statistical procedures within GMM.

1.46. This procedure standardized the size of the objects and optimized their rotation and translation so that the distances between corresponding landmarks were minimized. To summarize: variation among the landmark data configurations of all specimens shape the principal component analysis (PCA) – i.e., the relative warp analysis for parameter $\alpha = 0$ – was carried out in tpsRelw, ver. 1.46. (Rohlf, 2008). Then, we used the scores for the object of the first 15 axes describing 93% of total variation to test for the group shape differences by means of the two-group permutation test on Mahalanobis distance with 10,000 permutations (computed in PAST; Hammer, Harper, & Ryan, 2001).

To determine the shape variation associated with eye color, we regressed GPA shape coordinates onto eye color using multivariate regression in which shape coordinates is the dependent variable and eye color the independent variable (conducted in tpsRegr, ver. 1.36; Rohlf, 2009b). Shape regressions were displayed by thin-plate splines as deformation from the overall mean configuration (the consensus) of landmarks. Composite pictures were made using tpsSuper, ver. 1.14 (Rohlf, 2004): 3× magnified estimated shape configurations were used as fixed templates to which the pictures of 20 brown-eyed and 20 blue-eyed males were unwarped.

3. Results

Iris color had a significant effect on perceived dominance in males ($p = 0.031$; $\eta^2 = 0.108$); brown-eyed males were rated as more dominant than blue-eyed, Fig. 2. However, no effect was observed for perceived dominance in females ($p = 0.942$; $\eta^2 = 0.001$). After the age of the rated subjects was added into the GLM as a covariate, the effect of eye color on the perceived dominance of males decreased; however, the effect was still present ($p = 0.050$; $\eta^2 = 0.100$). The effect of age of the rated person was not significant ($p = 0.128$; one-tailed test).

In order to find out whether it is eye color that specifically influences perceived dominance in males, and not other eye color-associated facial features, we changed the iris color of brown-eyed

subjects to blue and vice versa. Changing the eye color had no effect on perceived naturalness of the manipulated photographs ($p = 0.345$; $\eta^2 = 0.023$; after adding age as covariate: $p = 0.356$; $\eta^2 = 0.023$). With this manipulation, males with eye color changed to blue (originally brown-eyed) were rated as more dominant than males with brown colored irises (originally blue-eyed). Nevertheless, this relation was not statistically significant ($p = 0.127$; $\eta^2 = 0.060$).

Clearer results were obtained by one sample *t*-test (that is in principle a paired test and therefore has higher statistical power). Mean differences of perceived dominance of subjects before and after eye color manipulation (–0.027 for blue-eyed subjects, 0.027 for brown-eyed subjects) were not different from zero (blue-eyed: $t = 0.222$, $df = 19$, $p = 0.826$; brown-eyed: $t = 0.171$, $df = 19$, $p = 0.866$), which suggests that the color of iris itself had no effect on perceived dominance.

The two-group permutation test for the GPA data rejected the null hypothesis of no association between facial shape and eye color. The effect of eye color on shape differences was clearly significant ($p = 0.0054$; Mahalanobis distance = 0.44; permutation $N = 10,000$). The shape regressions upon eye color visualized by thin-plate splines as predicted transformations in both directions from the consensus (mean) are shown in Fig. 3. The thin-plate spline deformations illustrate shape differences in the faces of blue-eyed and brown-eyed males. The grid deformations are especially visible on the differences in lateral compression (or dilations) in the chin, mouth, and eye region.

Our data suggested no relation between eye color and attractiveness, neither for rated photographs of males ($p = 0.678$; $\eta^2 = 0.005$) nor females ($p = 0.848$; $\eta^2 = 0.001$).

4. Discussion

In this study we found no effect of eye color on perceived dominance in women. On the contrary, we found a statistically significant association between the eye color and perceived dominance in men: brown-eyed men were perceived as more dominant.

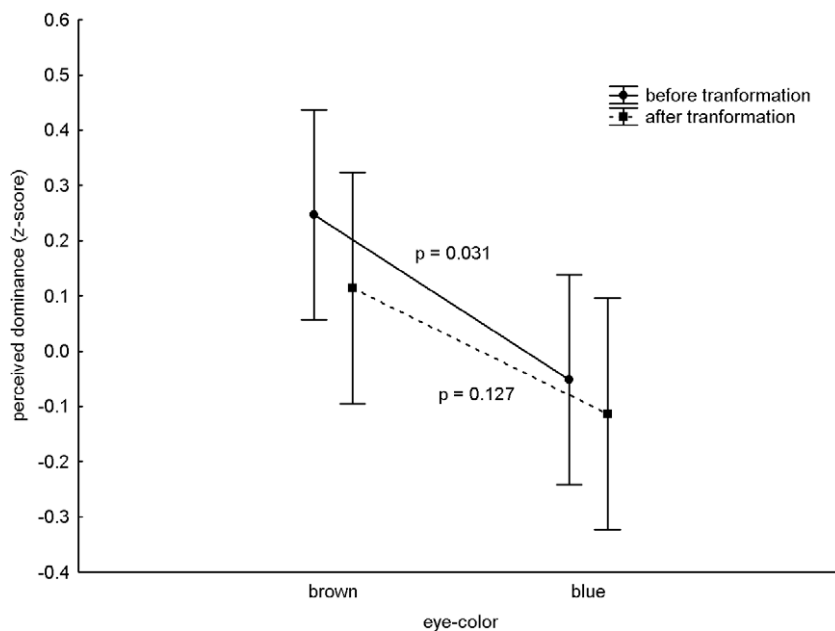


Fig. 2. Perceived dominance of males with iris color transformed from blue to brown and vice versa. Graph shows differences in perceived dominance of brown-eyed men (left) and blue-eyed men (right). The y-axis shows dominance expressed in Z-scores; whiskers denote standard deviations. (For interpretation of the references in colour in this figure legend, the reader is referred to the web version of this article.)

Furthermore, we show that iris color does *not* represent the trait that significantly influences perception of dominance in males. Hence, there must be some other facial characteristics responsible for the higher perceived dominance in brown-eyed males. It is evident, however, that the features standing for higher perceived dominance in males are correlated with presence of brown eyes; or alternatively, the features connected with higher perceived submissiveness in males with the blue eyes.

The question arises: why are brown-eyed males rated as more dominant than blue-eyed? Some facial features such as square jaws, thick eyebrows and broad cheekbones are linked with higher perceived dominance; facial submissiveness, on the other hand, is characterized by a round face with large eyes, smallish nose, and high eyebrows (Berry, 1990; Berry & McArthur, 1986; Cunningham, Barbee, & Pike, 1990; Mazur, Halpern, & Udry, 1994; Mueller & Mazur, 1997; Thornhill & Gangestad, 1994). The morphological differences between blue-eyed and brown-eyed males were visualized by deformation of thin-plate splines (Fig. 3). In contrast with blue-eyed males, brown-eyed males have statistically broader and rather massive chins, broader (laterally prolonged) mouths, larger noses, and eyes that are closer together with larger eyebrows. In contrast, blue-eyed males show smaller and sharper chins, mouths that are laterally narrower, noses smaller, and a greater span between the eyes. Especially the broader massive chin, bigger nose, and larger eyebrows of brown-eyed males may explain their higher perceived dominance.

However, it is not easy to explain how iris color, which is determined mostly by one or a few genes, can correlate with physiognomic dominance/submissiveness, which is determined by a combination of several independent morphological traits. Theoretically, the allele for brown eyes should “move” from “submissive physiognomy genotype” to “dominant physiognomy genotype” and back again from generation to generation due to genetic recombination and segregation.

In principle, there are three possible explanations for the higher perceived dominance of brown-eyed males, the pleiotropy hypothesis, genetic linkage hypothesis and social feedback hypothesis. The pleiotropy hypothesis presumes that the genes for iris color

(such as *HERC2* or *OCA2*) also influence other morphological traits associated with perceived dominance due to its pleiotropy effect. One can speculate, for instance, that the gene influences the production or metabolism of common precursors of adrenaline and melanin, e.g. DOPA or tyrosine.

The genetic linkage hypothesis presumes that the genes influencing iris color are in genetic linkage with genes influencing morphological traits associated with perceived dominance, for example the gene influencing the production of testosterone. If this is so, strong linkage disequilibrium between these loci should exist in the current Czech population. Repeating this study in other populations with polymorphism in eye color can test this hypothesis.

The social feedback hypothesis is based on the presumption that blue and brown-eyed subjects are treated differently within their social surroundings, e.g. by their parents and peers. Young children usually have blue eyes, while definitive iris color develops during the first years of life (Bito, Matheny, Cruickshanks, Nondahl, & Carino, 1997). It is possible that subjects with blue eyes are treated as a small child for a longer period than brown-eyed children. Such early social experience may have been literally “inscribed” into their faces, preserved until adulthood, and finally bring on the perception of higher submissiveness. Rosenberg and Kagan (1987, 1989) investigated the association between eye color and behavioral inhibition, revealing that children with blue eyes are more inhibited. Coplan et al. (1998) found a significant interaction between eye color and social wariness within preschoolers. Blue-eyed males were rated as more socially wary, i.e. being more temperamentally inhibited, displaying more reticent behavior and having more internalizing problems, than males with brown eyes, though there were no differences between blue- and brown-eyed females (Coplan et al., 1998). To test the third hypothesis, it would be necessary to perform a longitudinal study on preschool children to search whether the differences in perceived dominance (and social wariness) develops only after the transformation of iris color from blue to brown.

In this study, we did not observe any association between eye color and attractiveness, neither in men nor women, which seems to contradict the paternity-assurance hypothesis of the preference

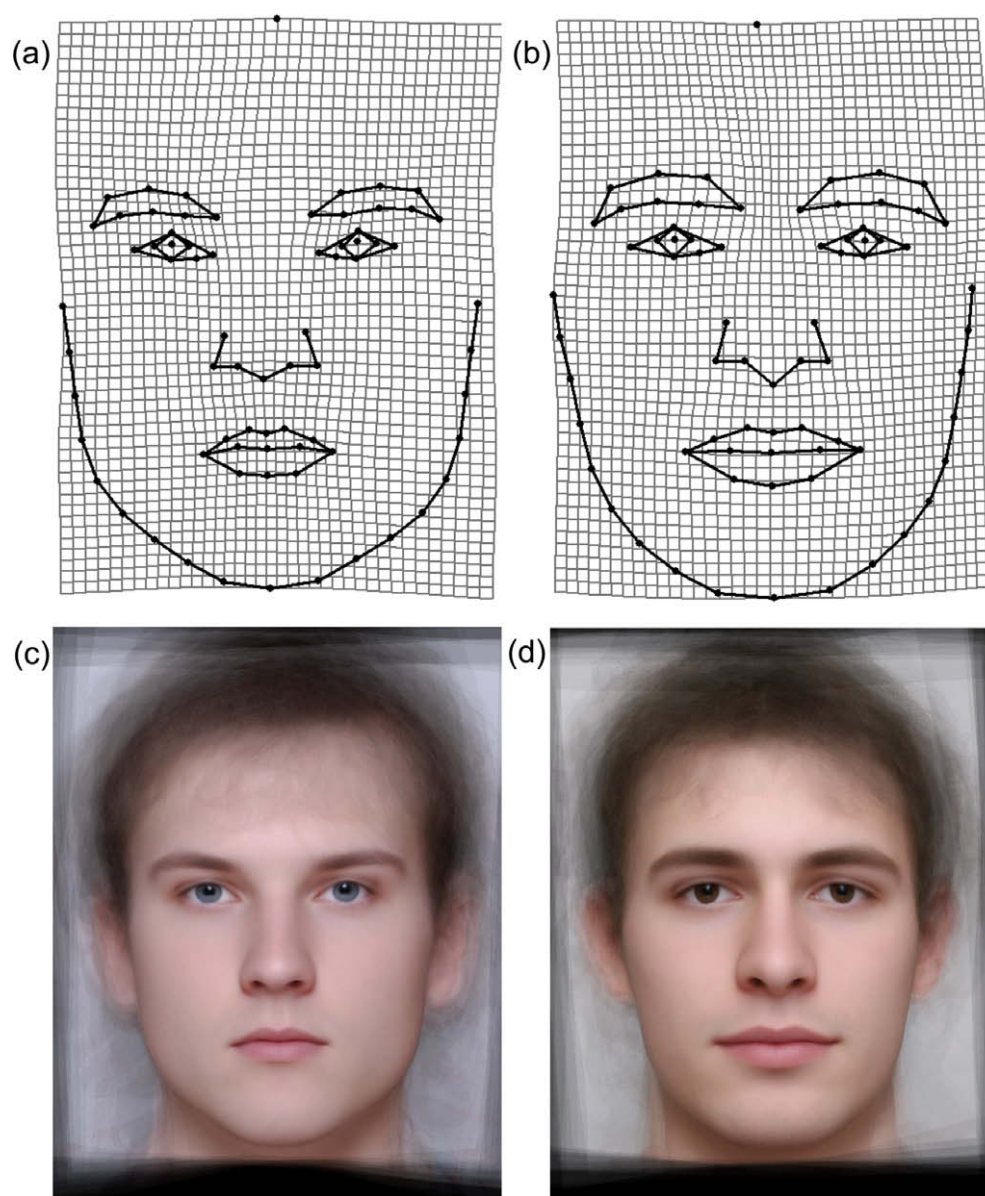


Fig. 3. (a and b): Visualizations of shape regression on eye color in males by thin-plate spline deformation grids illustrating differences in facial shape between blue-eyed (a) and brown-eyed (b) males; the links connecting the landmarks are drawn for better imaging of differences in the shape of face. (c and d): Composite images of 20 photographs of each group unwarped to fixed landmark configuration predicted by shape regression of blue-eyed (c) and brown-eyed (d) male faces. The predictions are magnified three times for better readability. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

of blue-eyed men for blue-eyed women (Laeng, Mathisen, & Johnsen, 2007). Attractiveness is usually associated with desirable personality traits (Langlois et al., 2000). The relationship of attractiveness and eye color may be obscured by the fact that brown eye color (or morphological traits of brown-eyed faces) is linked to perceived dominance, which is typically ascribed to masculine faces (Keating, 1985). It must be remembered, however, that male facial masculinity is a trait preferred in some circumstances or by some individuals, and at the same time disliked by others or in other circumstances. For example, female preferences differ in fertile and non-fertile phases of their menstrual cycle (Havlicek et al., 2005; Penton-Voak et al., 1999). Women in their fertile phase consider more dominant (masculine) men as more attractive and in non-fertile phases as less attractive. On the other hand, other authors have found that besides dominance, masculine features may indicate higher levels of rather undesirable traits, such as a lower willingness to invest in children, or higher aggressiveness

and antisocial behavior (Mazur & Booth, 1998). Thus, it is possible that we were not able to identify the relationship between attractiveness and brown eye color (settled in dominant-looking, i.e. masculine faces) because this would demand inspection of some other characteristics of the raters (such as menstrual cycle phase, or partnership status), which were not included in our study.

The most important question is whether eye color honestly reflects a dominant character in a man and therefore can be used by a female, for instance, as the indicator of dominance in a potential sexual or social partner. It has been suggested and demonstrated that women follow mixed mating strategy: they prefer dominant males as extra-pair sexual partners while at the same time they are seeking males who are more willing to invest in their offspring as long-term or social partners (Havlicek et al., 2005; Reynolds, 1996). To answer this important question, it would be necessary to search for a correlation between psychological dominance and iris color in future studies.

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References

- Bassett, J. F., & Dabbs, J. M. (2001). Eye color predicts alcohol use in two archival samples. *Personality and Individual Differences*, 31, 535–539.
- Berry, D. S. (1990). Taking people at face value – Evidence for the kernel of truth hypothesis. *Social Cognition*, 8, 343–361.
- Berry, D. S., & McArthur, L. Z. (1986). Perceiving character in faces – The impact of age-related craniofacial changes on social-perception. *Psychological Bulletin*, 100, 3–18.
- Bito, L. Z., Matheny, A., Cruickshanks, K. J., Nondahl, D. M., & Carino, O. B. (1997). Eye color changes past early childhood – The Louisville Twin Study. *Archives of Ophthalmology*, 115, 659–663.
- Bookstein, F. L. (1991). *Morphometric tools for landmark data: Geometry and biology*. New York: Cambridge University Press.
- Christensen, J. M., & Sacco, P. R. (1989). Association of hair and eye color with handedness and stuttering. *Journal of Fluency Disorders*, 14, 37–45.
- Coplan, R. J., Coleman, B., & Rubin, K. H. (1998). Shyness and little boy blue: Iris pigmentation, gender, and social wariness in preschoolers. *Developmental Psychobiology*, 32, 37–44.
- Cumming, R. G., Mitchell, P., & Lim, R. (2000). Iris color and cataract: The blue mountains eye study. *American Journal of Ophthalmology*, 130, 237–238.
- Cunningham, M. R., Barbee, A. P., & Pike, C. L. (1990). What do women want – Facial metric assessment of multiple motives in the perception of male facial physical attractiveness. *Journal of Personality and Social Psychology*, 59, 61–72.
- Dryden, I. L., & Mardia, K. V. (1998). *Statistical shape analysis*. New York: Wiley.
- Duffy, D. L., Montgomery, G. W., Chen, W., Zhao, Z. Z., Le, L., James, M. R., et al. (2007). A three-single-nucleotide polymorphism haplotype in intron 1 of OCA2 explains most human eye-color variation. *American Journal of Human Genetics*, 80, 241–252.
- Fink, B., Grammer, K., Mitteroecker, P., Gunz, P., Schaefer, K., Bookstein, F., et al. (2005). Second to fourth digit ratio and face shape. *Proceedings of the Royal Society B – Biological Sciences*, 272, 1995–2001.
- Hammer, O., Harper, D. A. T., & Ryan, P. D. (2001). PAST: Paleontological statistics software package for education and data analysis. *Palaeontologia Electronica*, 4, 9.
- Havlicek, J., Roberts, S. C., & Flegr, J. (2005). Women's preference for dominant male odour: Effects of menstrual cycle and relationship status. *Biology Letters*, 1, 256–259.
- Kagan, J., & Snidman, N. (2004). *The long shadow of temperament*. Cambridge, MA: Belknap Press.
- Kayser, M., Liu, F., Cecile, A., Janssens, J. W., Rivadeneira, F., Lao, O., et al. (2008). Three genome-wide association studies and a linkage analysis identify HERC2 as a human iris color gene. *American Journal of Human Genetics*, 82, 411–423.
- Keating, C. F. (1985). Gender and physiognomy of dominance and attractiveness. *Social Psychology Quarterly*, 48, 61–70.
- Kleisner, K. (2008a). Homosemiosis, mimicry and superficial similarity: Notes on the conceptualization of independent emergence of similarity in biology. *Theory in Biosciences*, 127, 15–21.
- Kleisner, K. (2008b). The semantic morphology of Adolf Portmann: A starting point for the biosemiotics of organic form? *Biosemiotics*, 1, 207–219.
- Kobayashi, H., & Kohshima, S. (1997). Unique morphology of the human eye. *Nature*, 387, 767–768.
- Kobayashi, H., & Kohshima, S. (2001). Unique morphology of the human eye and its adaptive meaning: Comparative studies on external morphology of the primate eye. *Journal of Human Evolution*, 40, 419–435.
- Laeng, B., Mathisen, R., & Johnsen, J. A. (2007). Why do blue-eyed men prefer women with the same eye color? *Behavioral Ecology and Sociobiology*, 61, 371–384.
- Langlois, J. H., Kalakanis, L. E., Rubenstein, A. J., Larson, A. D., Hallam, M. J., & Smoot, M. T. (2000). Maxims and myths of beauty: A meta-analytic and theoretical review. *Psychological Bulletin*, 126, 390–423.
- Liu, F., van Duijn, K., Vingerling, J. R., Hofman, A., Uitterlinden, A. G., Janssens, A. J. W., et al. (2009). Eye color and the prediction of complex phenotypes from genotypes. *Current Biology*, 19, R192–R193.
- Mazur, A., & Booth, A. (1998). Testosterone and dominance in men. *Behavioral and Brain Sciences*, 21, 353–397.
- Mazur, A., Halpern, C., & Udry, J. R. (1994). Dominant looking male teenagers copulate earlier. *Ethology and Sociobiology*, 15, 87–94.
- Mitteroecker, P., & Gunz, P. (2009). Advances in geometric morphometrics. *Evolutionary Biology*, 36, 235–247.
- Mueller, U., & Mazur, A. (1997). Facial dominance in Homo sapiens as honest signaling of male quality. *Behavioral Ecology*, 8, 569–579.
- Penton-Voak, I. S., Perrett, D. I., Castles, D. L., Kobayashi, T., Burt, D. M., Murray, L. K., et al. (1999). Menstrual cycle alters face preference. *Nature*, 399, 741–742.
- Regan, S., Judge, H. E., Gragoudas, E. S., & Egan, K. M. (1999). Iris color as a prognostic factor in ocular melanoma. *Archives of Ophthalmology*, 117, 811–814.
- Reynolds, J. D. (1996). Animal breeding systems. *Trends in Ecology and Evolution*, 11, 68–72.
- Rohlf, J. F. (2004). *TpsSuper (version 1.14)*. New York: Department of Ecology and Evolution, State University of New York at Stony Brook.
- Rohlf, J. F. (2008). *TpsRelw (version 1.46)*. New York: Department of Ecology and Evolution, State University of New York at Stony Brook.
- Rohlf, J. F. (2009a). *TpsDig2 (version 2.14)*. New York: Department of Ecology and Evolution, State University of New York at Stony Brook.
- Rohlf, J. F. (2009b). *TpsRegr (version 1.36)*. New York: Department of Ecology and Evolution, State University of New York at Stony Brook.
- Rosenberg, A., & Kagan, J. (1987). Iris pigmentation and behavioral inhibition. *Developmental Psychobiology*, 20, 377–392.
- Rosenberg, A., & Kagan, J. (1989). Physical and physiological correlates of behavioral inhibition. *Developmental Psychobiology*, 22, 753–770.
- Schaefer, K., & Bookstein, F. L. (2009). Does geometric morphometrics serve the needs of plasticity research? *Journal of Biosciences*, 34, 589–599.
- Slice, D. E. (Ed.). (2005). *Modern morphometrics in physical anthropology*. New York: Kluwer Academic/Plenum Press.
- Schaefer, K., Grammer, K., Fink, B., Mitteroecker, P., Gunz, P., & Bookstein, F. L. (2006). Female appearance: Facial and bodily attractiveness as shape. *Psychology Science*, 48, 178–205.
- Thornhill, R., & Gangestad, S. W. (1994). Human fluctuating asymmetry and sexual-behavior. *Psychological Science*, 5, 297–302.
- Tomasello, M., Hare, B., Lehmann, H., & Call, J. (2007). Reliance on head versus eyes in the gaze following of great apes and human infants: The cooperative eye hypothesis. *Journal of Human Evolution*, 52, 314–320.
- Zebrowitz, L. A. (1997). *Reading faces: Windows to the soul?* Boulder, CO: Westview Press.
- Zelditch, M. L., Swiderski, D. L., Sheets, D. H., & Fink, W. L. (2004). *Geometric morphometrics for biologists: A primer*. London: Elsevier.