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An Empirical Investigation on the Sexual Selection Hypothesis of Human Phenotypic Diversity: A Test in Okinawa and Mainland Japan

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Sexual selection may have played a role in the formation and maintenance of phenotypic diversity among human populations. A theoretical study has shown that phenotypic diversification between neighboring populations connected by gene flow can occur if individuals have a mating preference for typical characteristics of their population (i.e., own-group preference), or if preferences are culturally transmitted only between the members of the same population (i.e., model-dependent mate-choice copying). To date, however, empirical investigation is lacking on the presence or absence of own-group preference and model-dependent mate-choice copying in neighboring populations exhibiting phenotypic differentiation. Here we report the results of an experiment on preference for faces in Okinawa Islanders and Mainland Japanese as an example of such populations. It was suggested that female Okinawa Islanders tend to prefer male faces of their own population to those of Mainland Japanese, and male Okinawa Islanders' evaluation of faces is affected more by members of their own population than those of the other. These findings support the argument that the phenotypic difference between Okinawa Islanders and Mainland Japanese may be partially explicable by sexual selection.

Keywords
assortative mating, facial attractiveness, gene-culture coevolution, mate-choice copying, own-group preference, social learning

Introduction

Despite the small genetic differentiation between populations in humans as compared to great apes (Enard & Pääbo, 2004; Fischer et al., 2004), phenotypic variations among human populations do exist (e.g., skin color, Jablonski & Chaplin, 2010; craniofacial metrics, Roseman, 2004). This indicates the presence of natural and/or sexual selection diversifying populations against considerable gene flow. While studies have examined the effect of natural selection on human phenotypic differentiation (Harvati & Weaver, 2006; Relethford, 2010), the effect of sexual selection has rarely been investigated, partly because mate choice is thought to impose directional rather than disruptive selection. However, sexual selection is expected to diversify populations if mating preferences vary between populations (i.e., the sexual selection hypothesis). Nojo & Ihara's (2019) computer simulation has demonstrated that sexual selection can indeed cause phenotypic diversification between neighboring populations in the presence of gene flow if individuals prefer the average phenotypic value of their own population or an arbitrary value that is culturally transmitted within population.

While theoretically coherent, the sexual selection hypothesis needs further scrutiny in terms of empirical plausibility. Specifically, whether human individuals have such preferences as assumed in Nojo & Ihara (2019) is so far unclear. Preference for the population average was partly shown by Sofer et al. (2017) for facial characteristics. They examined Israeli and Japanese women's preference over a spectrum of morphed facial images, with Israeli- and Japanese-typical faces being the two ends of the spectrum. Women from both populations tended to judge those faces typical of their own population more trustworthy, although mixed-population faces were perceived as more attractive. In any case, the phenotypic difference between the Israeli and Japanese populations is not an ideal example to be explained by sexual selection, because they are geographically so distant that the difference seems explicable either by random drift or local adaptation.

This study focuses on the facial difference between the Okinawa and mainland populations of Japan as a possible example of phenotypic diversification driven by sexual selection. Studies have documented distinct features in the residents of Okinawa prefecture, located at the southwestern end of Japan, relative to those of other parts of Japan, including genetic (Omoto & Saitou, 1997; Yamaguchi-Kabata et al., 2008; HUGO Pan-Asian SNP Consortium, 2009), cultural (Shibatani, 1990), and craniofacial (Hanihara, 1991; Miyazato et al., 2014) characteristics. Apparently, there is substantial gene flow between the two populations: roughly two percent of the Okinawa population move out each year and about the same number of people move in from the mainland (https://www.e-stat.go.jp/en). If sexual selection has played a role in phenotypically diversifying the two populations, it is expected that people in Okinawa and/or those in the mainland have the kind of mating preference as assumed

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in Nojo & Ihara (2019). To explore this possibility, we ask (i) whether people from the Okinawa and mainland populations tend to prefer faces of their own population, and (ii) whether their preferences are socially more affected by the members of their own population than by those of the other population.

Methods

Subjects & stimuli

We defined people who themselves and whose parents had all been born in Okinawa prefecture as Okinawa Islanders (OI), and residents of the Tokyo area who themselves and whose parents had all been born in any Japanese prefecture other than Okinawa as Mainland Japanese in Tokyo (MJT). As OI participants, 60 men (18–40 years old, mean = 20.65, *SD* = 5.06) and 60 women (18–40 years old, mean = 21.08, *SD* = 5.89) were recruited at Okinawa College of Rehabilitation and Welfare. As MJT participants, 81 men (18–28 years old, mean = 19.78, *SD* = 13.32) and 39 women (19–21 years old, mean = 19.41, *SD* = 0.56) were recruited at the University of Tokyo.

We also collected facial photographs of 30 OI men (19–35 years old, mean = 28.17, *SD* = 4.79), 30 OI women (18–40 years old, mean = 27.94, *SD* = 6.04), 30 MJT men (21–39 years old, mean = 29.14, *SD* = 5.64), and 30 MJT women (18–38 years old, mean = 26.48, *SD* = 6.25) with neutral facial expressions from anterior view and both sides of lateral views. From these photographs, we made 20 "target faces" of each sex (anterior view) by averaging three randomly selected faces with Psychomorph software (Tiddeman et al., 2001). In addition, five photographs for each of OI men, MJT men, OI women, and MJT women played the role as "model faces." To remove the effect of hairstyle and clothes, outside of the contour of all stimuli was painted in black.

Own-group preference

Our experiment consisted of three sections. Section 1 was to examine whether people have a preference for faces of their own population. Participants were handed out sheets of questionnaire and rated opposite-sex target faces using an 11-point scale from 0 to 10 (0 for least and 10 for most), where each target was presented on a separate sheet in a random order. They were asked to rate targets in three contexts: attractiveness as a long-term partner (e.g., for marriage), attractiveness as a short-term partner (e.g., for a single date), and trustworthiness. Participants read a Japanese translation of Perrett et al.'s (2002) definitions of long-term and short-term attractiveness. To ensure participants' understanding of the three contexts, we gave an additional verbal instruction immediately before the rating and presented the sheets of questionnaire for the three contexts in the same order as instructed to all participants.

Mate-choice copying

We hypothesized that the participants' ratings on faces would be altered after observing other people's (i.e., models') evaluation on the same faces and that this effect would be more salient when the models belonged to the same population as the participants. However, the social effect on a participant's judgement may depend not only on the models' group identity, but also on their individual characteristics, such as attractiveness. Taking this possibility into consideration, we examined the social effect of model's ratings after controlling for variation in model's individual characteristics. For that purpose, in Section 2, we measured sexual attractiveness and trustworthiness of model faces. Each participant rated ten model faces (anterior and lateral views) consisting of five OI and five MJT faces, all of whom were of the same sex as the participant, using the 11-point scales for sexual attractiveness and trustworthiness. These scores were incorporated as an independent variable of the regression equation in the analysis of mate-choice copying (see Statistical analysis). Each model was presented in a separate sheet (Figure 1).

About an hour after the end of the first section, Section 3 took place to evaluate the social effect on participants' ratings. Each participant rated the same set of targets in the same way as in Section 1, except that this time each target was presented with four model faces of the same sex as the participant and a fictive "average rating" (Figure 2). The models were introduced as the persons who had given the ratings from which the average rating was calculated, but in fact they were chosen at random from the five OI faces or from the five MJT faces that the participant rated in Section 2. The values shown as the average ratings were chosen randomly from 7 to 10, which were considerably higher than the actual average ratings given by the participants. Thus, regarding an increase in the score from Sections 1 to 3 as indicative of the social effect, we used the score in Section 3 subtracted by the score in Section 1 as a measure of mate-choice copying. Of the ten targets made from OI faces, five were presented with OI models and the other five with MJT models; similarly, five of the targets made from MJT faces were shown with OI models and the other five with MJT models. OI and MJT models were presented in a random order.

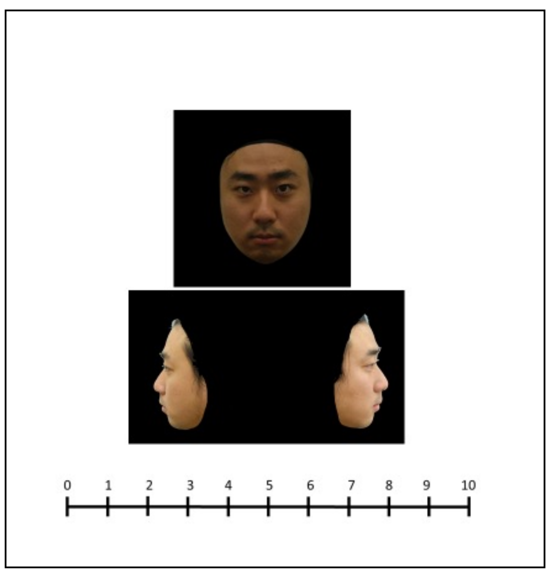

Figure 1. A sample sheet of questionnaire used in Section 2 (for illustration purposes only).

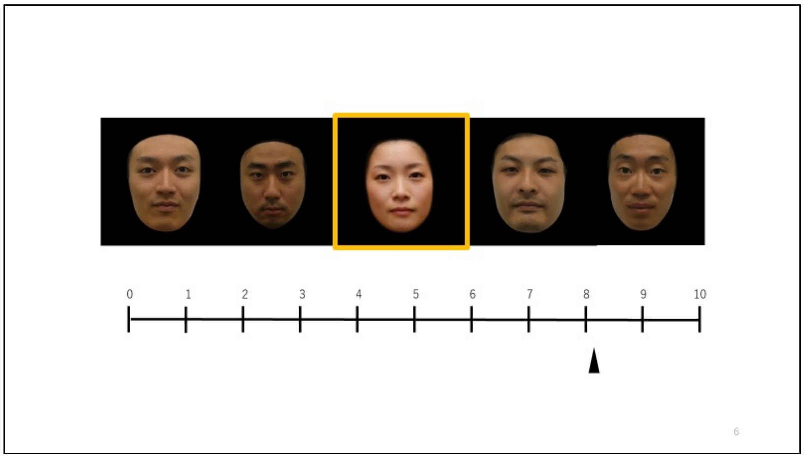

Figure 2. A sample sheet of questionnaire used in Section 3 (for illustration purposes only).

Statistical analysis

For statistical analysis, we applied the hierarchical Bayesian modeling, separately for male and female participants and for the three contexts. In the analysis of own-group preference, a participant's rating on a target in Section 1 was regressed on dummy variables for the target's and participant's populations and the interaction of the two variables. We assumed a linear model with a normally distributed error term and the identity link function. Formally, the ith participant's rating on the jth target, denoted by y_{ij}, was predicted by the following equation:

$$y_{ij} = b_0 + b_1 x_{Tj} + b_2 x_{Pi} + b_3 x_{Tj} x_{Pi} + r_{Pi} + r_{Tj},$$

where x_{Tj} and x_{Pi} are dummy variables coding for the the jth target's and the ith participant's populations, respectively (0.5 for OI and −0.5 for MJT). To consider within-population variation in the ratings, we incorporated random effects of the ith participant and the jth target, r_{Pi} and r_{Tj}, respectively, which were assumed to be normally distributed with mean zero and standard deviations s_1 and s_2.

In the analysis of mate-choice copying, a participant's rating on a target in Section 1 was subtracted from that in Section 3, and this difference was regressed on dummy variables for the participant's and model's populations, their interaction, and the average attractiveness rating of the four models given by the participant in Section 2. Note that since attractiveness and trustworthiness scores given to a model were positively correlated in female (r = .43, N = 20, p < .05) and male models (r = .82, N = 20, p < .0001), we included only attractiveness in the following analysis, but it was confirmed that the results were essentially the same when trustworthiness instead of attractiveness was used. Let z_{ijk} denote the ith participant's rating on the jth target when presented with the kth tetrad of models. The difference of the ratings between Sections 1 and 3 was described by the following equation:

$$z_{ijk} - y_{ij} = b_0 + b_1 x_{Mk} + b_2 x_{Pi} + b_3 w_{ik} + b_4 x_{Mk} x_{Pi} + r_{Pi} + r_{Tj},$$

where x_{Mk} is a dummy variable for the population of the kth tetrad of models (0.5 for OI and −0.5 for MJT). We introduced w_{ik}, the average of the ith participant's ratings on the attractiveness of the kth tetrad of models to control for the variation in the attractiveness of models.

We assumed noninformative prior and hyperprior distributions for b_m and s_m, respectively. Posterior distributions of the parameters were estimated by Markov chain Monte Carlo (MCMC) method with three replicated sampling, each of which contained 10000 iterations, using brm package in R 3.5.0 (Bürkner, 2017, 2018). The Rhat of the estimated parameter was all under 1.05, suggesting sufficient iterations of the MCMC sampling. The last 5000 of the 10000 iterations were used to estimate the posterior distributions of the parameters, and their means are reported below as the estimates. Statistical significance was evaluated on the basis of the 95% credible interval (CI) of the posterior distribution.

Results

Since some MJT participants were dropped before Section 3, we included 141 men and 99 women in the analysis of own-group preference and 127 men and 90 women in the analysis of mate-choice copying.

Own-group preference

Figure 3 shows the means and standard deviations of the ratings in Section 1. Table 1 shows parameter estimates for the analysis of own-group preference. Significant main effect of target's population on the women's ratings for trustworthiness was found (b_1 = 0.57), where OI targets were rated higher than MJT targets. We also found significant main effects of participant's population in the female participants for long-term attractiveness (b_2 = −0.76) and trustworthiness (b_2 = −0.89), and in the male participants for long-term (b_2 = −0.54) and short-term (b_2 = −0.64) attractiveness, where the negative values indicate lower ratings for OI than MJT participants. We observed significant interactions between participant's and target's populations in the female participants for long-term attractiveness (b_3 = 0.32) and trustworthiness (b_3 = 0.46), where the women rated targets of their own population higher. Results shown in Figure 3 are consistent with the interpretation that both OI and MJT participants prefer OI to MJT faces, while OI faces are preferred more by OI than MJT women for long-term attractiveness and trustworthiness. Similar results were obtained when we

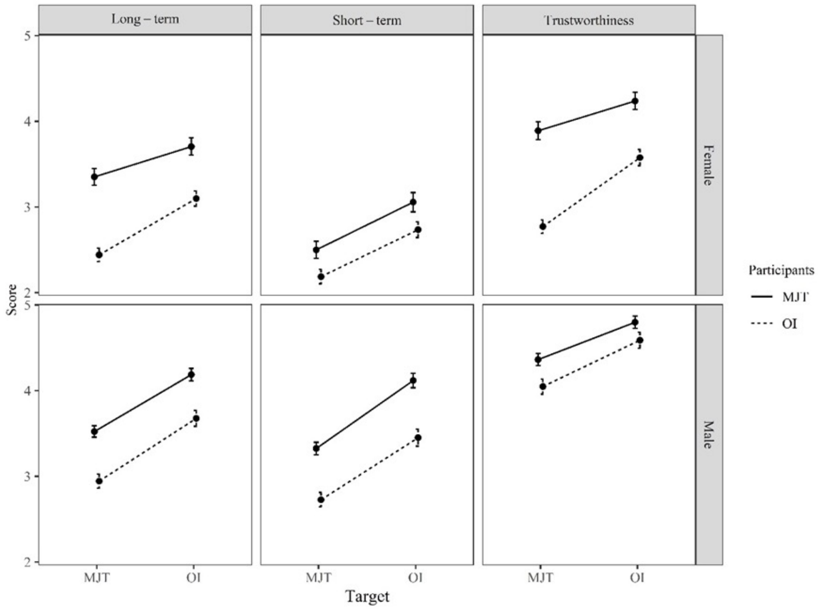

Figure 3. Means and standard deviations of the ratings in Session 1.

Table 1. MCMC estimates of parameters for the analysis of own-group preference.

Participant's sex	Context	Parameter	Estimate	95% CI
Female	Long-term	b_0 (intercept)	3.16	[2.74, 3.36]
		b_1 (target population)	0.51	[−0.10, 1.11]
		b_2 (participant population)	−0.76	[−1.33, −0.18]
		b_3 (interaction)	0.32	[0.07, 0.57]
		s_1 (participant SD)	1.38	[1.19, 1.60]
		s_2 (target SD)	0.65	[0.46, 0.94]
	Short-term	b_0 (intercept)	2.61	[2.18, 3.03]
		b_1 (target population)	0.56	[−0.02, 1.13]
		b_2 (participant population)	−0.32	[−0.97, 0.34]
		b_3 (interaction)	−0.02	[−0.27, 0.23]
		s_1 (participant SD)	1.56	[1.35, 1.81]
		s_2 (target SD)	0.62	[0.44, 0.90]
	Trustworthiness	b_0 (intercept)	3.62	[3.27, 3.97]
		b_1 (target population)	0.57	[0.10, 1.05]
		b_2 (participant population)	−0.89	[−1.43, −0.34]
		b_3 (interaction)	0.46	[0.17, 0.75]
		s_1 (participant SD)	1.32	[1.14, 1.54]
		s_2 (target SD)	0.49	[0.34, 0.72]
Male	Long-term	b_0 (intercept)	3.58	[3.09, 4.07]
		b_1 (target population)	0.70	[−0.18, 1.56]
		b_2 (participant population)	−0.54	[−1.02, −0.05]
		b_3 (interaction)	0.07	[−0.12, 0.26]
		s_1 (participant SD)	1.42	[1.25, 1.60]
		s_2 (target SD)	0.96	[0.68, 1.38]
	Short-term	b_0 (intercept)	3.41	[2.88, 3.92]
		b_1 (target population)	0.77	[−0.14, 1.69]
		b_2 (participant population)	−0.64	[−1.18, −0.10]
		b_3 (interaction)	−0.07	[−0.27, 0.14]
		s_1 (participant SD)	1.58	[1.40, 1.78]
		s_2 (target SD)	0.99	[0.71, 1.43]
	Trustworthiness	b_0 (intercept)	4.44	[4.01, 4.86]
		b_1 (target population)	0.49	[−0.22, 1.20]
		b_2 (participant population)	−0.24	[−0.71, 0.22]
		b_3 (interaction)	0.10	[−0.12, 0.32]
		s_1 (participant SD)	1.38	[1.21, 1.56]
		s_2 (target SD)	0.79	[0.56, 1.14]

used lateral-view along with anterior-view target faces (Supplementary Materials S1).

Mate-choice copying

Figure 4 shows the means and standard deviations of the ratings in Session 3 subtracted by the ratings in Session 1. In all cases, the mean increase of the rating was positive. This suggests that the participants' ratings in Section 3 were affected by the fictive "average ratings" by the models, which were set to be considerably higher than the actual ratings by the participants (see also Supplementary Materials S2 and S3). Table 2 shows parameter estimates for the analysis of mate-choice copying. Model's population had a significant effect on the increase in the men's ratings from Sessions 1 to 3 for short-term attractiveness (b_1 = 0.18), suggesting that the male participants were more affected by OI than MJT models. A significant main effect was also observed for participant's population on the increase in the men's ratings for long-term attractiveness (b_2 = −0.64), where MJT men were more affected by the models than OI men were. Significant interactions between model's and participant's populations were found in the women's judgements for short-term attractiveness (b_4 = −0.38) and the men's judgement for trustworthiness (b_4 = 0.34), indicating that the women's judgements were less affected and the men's judgements were more affected by the models from their own population than by the models from the other population. In no case, model's attractiveness had a significant effect. When the analysis was repeated using model's trustworthiness instead of attractiveness, the results were qualitatively the same: the same set of parameters had statistically significant effects of the same directions (data not shown).

Discussion

Our experiment aimed to examine two hypotheses: people have own-group preference for faces, and people's preference for faces is affected more by members of their own population than by those of other populations. Our results provide partial support for both hypotheses.

Own-group preference was seen in women for long-term attractiveness and trustworthiness. Considering that both long-term attractiveness and trustworthiness are relevant to the choice of marriage partners, the female preference may enhance endogamy. While Sofer et al. (2017) showed own-group preference for faces at the level of countries, we found a similar tendency at the level of subpopulations within a country. On the other hand, we did not find similar own-group preference among men. The sex-dependent manifestation of own-group preference might be understood in the light of the general principle that it is the female whose choosiness has a significant impact on fitness.

We also found that a person's judgement on a face is affected differently by other people's judgement depending on whether they are members of the person's own population or those of other populations. Specifically, our results suggest that men tend to copy the judgement by own-group members about trustworthiness. This is congruent with the findings in non-human animals that an individual's mate-choice decisions are affected by observing choices of other individuals, but less so by social models with a characteristic that is atypical to the species (Kniel et al., 2017). On the other hand, it is also indicated that women are more affected by out-group than in-group members for short-term attractiveness. This result is unexpected, but might be understood as a part of female strategy to increase genetic diversity among short-term partners (DeBruine, 2005). Our results suggest the possibility that mate-choice copying work differently between males and females.

Combined with Nojo & Ihara's (2019) simulation study, the results of the present study suggest that

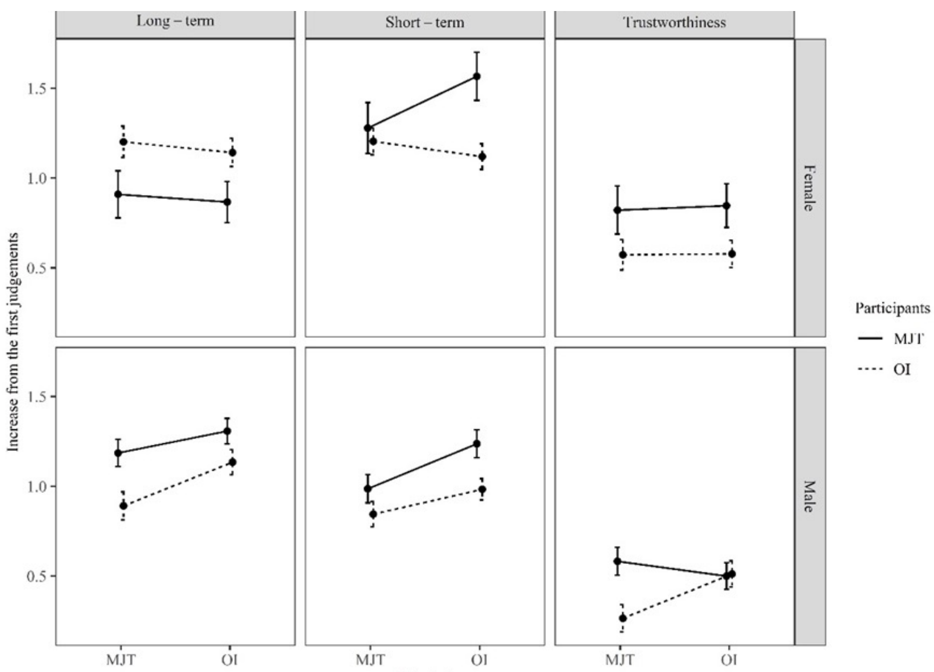

Figure 4. Means and standard deviations of the ratings in Session 3 subtracted by the ratings in Session 1.

Table 2. MCMC estimates of parameters for the analysis of mate-choice copying.

Participant's sex	Context	Parameter	Estimate	95% CI
Female	Long-term	b_0 (intercept)	1.11	[0.57, 1.64]
		b_1 (model population)	−0.04	[−0.24, 0.15]
		b_2 (participant population)	0.24	[−0.41, 0.88]
		b_3 (model attractiveness)	−0.02	[−0.13, 0.09]
		b_4 (interaction)	−0.02	[−0.33, 0.29]
		s_1 (participant SD)	1.42	[1.22, 1.67]
		s_2 (target SD)	0.13	[0.01, 0.26]
	Short-term	b_0 (intercept)	1.24	[0.72, 1.77]
		b_1 (model population)	0.11	[−0.11, 0.32]
		b_2 (participant population)	−0.25	[−0.87, 0.37]
		b_3 (model attractiveness)	0.01	[−0.09, 0.12]
		b_4 (interaction)	−0.38	[−0.69, −0.07]
		s_1 (participant SD)	1.28	[1.09, 1.51]
		s_2 (target SD)	0.15	[0.03, 0.22]
	Trustworthiness	b_0 (intercept)	0.68	[0.16, 1.18]
		b_1 (model population)	0.02	[−0.18, 0.21]
		b_2 (participant population)	−0.26	[−0.81, 0.31]
		b_3 (model attractiveness)	0.01	[−0.10, 0.12]
		b_4 (interaction)	−0.01	[−0.34, 0.32]
		s_1 (participant SD)	1.19	[1.00, 1.41]
		s_2 (target SD)	0.10	[0.01, 0.23]
Male	Long-term	b_0 (intercept)	0.76	[0.37, 1.16]
		b_1 (model population)	0.06	[−0.12, 0.25]
		b_2 (participant population)	−0.64	[−1.08, −0.19]
		b_3 (model attractiveness)	0.04	[−0.05, 0.13]
		b_4 (interaction)	−0.02	[−0.34, 0.14]
		s_1 (participant SD)	1.19	[1.04, 1.37]
		s_2 (target SD)	0.14	[0.03, 0.25]
	Short-term	b_0 (intercept)	0.85	[0.49, 1.22]
		b_1 (model population)	0.18	[0.02, 0.34]
		b_2 (participant population)	−0.15	[−0.60, 0.30]
		b_3 (model attractiveness)	0.04	[−0.04, 0.13]
		b_4 (interaction)	−0.11	[−0.33, 0.11]
		s_1 (participant SD)	1.22	[1.07, 1.39]
		s_2 (target SD)	0.12	[0.03, 0.22]
	Trustworthiness	b_0 (intercept)	0.40	[0.01, 0.79]
		b_1 (model population)	0.08	[−0.24, 0.41]
		b_2 (participant population)	−0.13	[−0.51, 0.25]
		b_3 (model attractiveness)	0.02	[−0.07, 0.11]
		b_4 (interaction)	0.34	[0.09, 0.58]
		s_1 (participant SD)	1.01	[0.88, 1.17]
		s_2 (target SD)	0.33	[0.21, 0.49]

sexual selection may be partially responsible for the emergence and/or maintenance of the difference in facial morphology between Okinawa Islanders and Mainland Japanese. Further research with a more comprehensive survey on people's preference is clearly needed to better understand the psychological mechanisms underlying the human phenotypic variations as a product of cultural diversification.

Acknowledgements

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Author contribution

S.N. and Y.I. designed the research and wrote the draft of the manuscript. S.N., R.K., and Y.I. collected the data. S.N. performed the analysis. All authors commented on the manuscript, revised it, and approved the final report.

Ethical statement

All study participants provided informed consent, and the study design was approved by research ethics committee of University of Tokyo (17-20).

Data accessibility & program code

The code and data used in this study is available in a GitHub repository (https://github.com/nojos/matechoicecopying.git).

Supplementary material

Electronic supplementary material is available online.

References

Bürkner, P.-C. (2017). brms: An R package for Bayesian multilevel models using Stan. *Journal of Statistical Software*, *80*(1), 1–28. https://doi.org/10.18637/jss.v080.i01

Bürkner, P.-C. (2018). Advanced Bayesian multilevel modeling with the R package brms. *R Journal*, *10*(1), 395–411. https://doi.org/10.32614/RJ-2018-017

DeBruine, L. M. (2005). Trustworthy but not lust-worthy: Context-specific effects of facial resemblance. *Proceedings of the Royal Society B: Biological Sciences*, *272*(1566), 919–922. https://doi.org/10.1098/rspb.2004.3003

Enard, W., & Pääbo, S. (2004). Comparative primate genomics. *Annual Reviews of Genomics and Human Genetics*, *5*, 351–378. https://doi.org/10.1146/annurev.genom.5.061903.180040

Fischer A., Wiebe, V., Pääbo, S., & Przeworski, M. (2004). Evidence for a complex demographic history of chimpanzees. *Moleculer Biology and Evolution*, *21*(5), 799–808. https://doi.org/10.1093/molbev/msh083

Hanihara, K. (1991). Dual structure model for the population history of the Japanese. *Japan Review*, *2*, 1–33. https://doi.org/10.15055/00000397

Harvati, K., & Weaver, T. D. (2006). Human cranial anatomy and the differential preservation of population history and climate signatures. *The Anatomical Record Part A, 288A*(12), 1225–1233. https://doi.org/10.1002/ar.a.20395

Jablonski, N. G., & Chaplin, G. (2010). Human skin pigmentation as an adaptation to UV radiation. *Proceedings of the National Academy of Sciences of the United States of America*, *107*(Supplement 2), 8962–8968. https://doi.org/10.1073/pnas.0914628107

HUGO Pan-Asian SNP Consortium, Abdulla, M. A., Ahmed, I., Assawamakin, A., Bhak, J., Brahmachari, S. K., Calacal, G. C., Chaurasia, A., Chen, C.-H., Chen, J., Chen, Y.-T., Chu, J., Cutiongco-de la Paz, E. M., De Ungria, M. C. A., Delfin, F. C., Edo, J., Fuchareon, S., Ghang, H., Gojobori, T., ... Zilfalil, B. A. (2009). Mapping human genetic diversity in Asia. *Science*, *326*(5959), 1541–1545. https://doi.org/10.1126/science.1177074

Kniel, N., Müller, K., & Witte, K. (2017). The role of the model in mate-choice copying in female zebra finches. *Ethology*, *123*(6–7), 412–418. https://doi.org/10.1111/eth.12611

Miyazato, E., Yamaguchi, K., Fukase, H., Ishida, H., & Kimura, R. (2014). Comparative analysis of facial morphology between Okinawa Islanders and mainland Japanese using three-dimensional images. *American Journal of Human Biology*, *26*(4), 538–548. https://doi.org/10.1002/ajhb.22560

Nojo, S., & Ihara, Y. (2019). The effect of sexual selection on phenotypic diversification among human populations: A simulation study. *Journal of Theoretical Biology*, *462*, 43476. https://doi.org/10.1016/j.jtbi.2018.10.058

Omoto, K., & Saitou, N. (1997). Genetic origins of the Japanese: A partial support for the dual structure hypothesis. *American Journal of Physical Anthropology*, *102*(4), 437–446. https://doi.org/10.1002/(SICI)1096-8644(199704)102:4%3C437::AID-AJPA1%3E3.0.CO;2-P

Perrett, D. I., Penton-Voak, I. S., Little, A. C., Tiddeman, B. P., Burt, D. M., Schmidt, N., Oxley, R., Kinloch, N., & Barrett, L. (2002). Facial attractiveness judgements reflect learning of parental age characteristics. *Proceedings of the Royal Society of London. Series B*, *269*(1494), 873–880. https://doi.org/10.1098/rspb.2002.1971

Relethford, J. H. (2010). Population-specific deviations of global human craniometric variation from a neutral model. *American Journal of Physical Anthropology*, *142*(1), 105–111. https://doi.org/10.1002/ajpa.21207

Roseman, C. C. (2004). Detecting interregionally diversifying natural selection on modern human cranial form by using matched molecular and morphometric data. *Proceedings of the National Academy of Sciences of the United States of America*, *101*(35), 12824–12829. https://doi.org/10.1073/pnas.0402637101

Shibatani, M. (1990). *The languages of Japan*. Cambridge University Press.

Sofer, C., Dotsch, R., Oikawa, M., Oikawa, H., Wigboldus, D. H. J., & Todorov, A. (2017). For your local eyes only: Culture-specific face typicality influences perceptions of trustworthiness. *Perception*, *46*(8), 914–928. https://doi.org/10.1177/0301006617691786

Tiddeman, B. P., Burt, D. M., & Perrett, D. I. (2001). Prototyping and transforming facial textures for perception research. *IEEE Computer Graphics and Applications*, *21*(5), 42–50. https://doi.org/10.1109/38.946630

Yamaguchi-Kabata, Y., Nakazono, K., Takahashi, A., Saito, S., Hosono, N., Kubo, M., Nakamura, Y., & Kamatani, N. (2008). Japanese population structure, based on SNP genotypes from 7003 individuals compared to other ethnic groups: Effects on population-based association studies. *American Journal of Human Genetics*, *83*(4), 445–456. https://doi.org/10.1016/j.ajhg.2008.08.019