Research Article

Variation in Women's Preferences Regarding Male Facial Masculinity Is Better Explained by Genetic Differences Than by Previously Identified Context-Dependent Effects

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Abstract
Women's preferences for masculine versus feminine male faces are highly variable. According to a dominant theory in evolutionary psychology, this variability results from adaptations that optimize preferences by calibrating them to certain contextual factors, including women's self-perceived attractiveness, short- versus long-term relationship orientation, pathogen disgust sensitivity, and stage of the menstrual cycle. The theory does not account for the possible contribution of genetic variation on women's facial masculinity preference. Using a large sample ($N = 2,160$) of identical and nonidentical female Finnish twins and their siblings, we showed that the proportion of variation in women's preferences regarding male facial masculinity that was attributable to genetic variation (38%) dwarfed the variation due to the combined effect of contextual factors (< 1%). These findings cast doubt on the importance of these context-dependent effects and may suggest a need for refocusing in the field toward understanding the wide genetic variation in these preferences and how this variation relates to the evolution of sexual dimorphism in faces.

Women's preferences for masculine versus feminine male faces are highly variable. A key pursuit of evolutionary psychologists has been to understand this variability. The dominant explanation focuses on a trade-off that women are thought to face when choosing a mate. This trade-off is between greater genetic quality ("good genes"), hypothesized to be associated with more masculine male faces, and greater parental quality ("good dad"), hypothesized to be associated with more feminine male faces. Mating with a man who has a masculine face is thought to confer genetic benefits to the offspring (which would increase the woman's inclusive fitness) and to decrease paternal investment in the children (which would decrease the woman's inclusive fitness). The theory is that the variability in women's preferences for facial masculinity or femininity is context-dependent: That is, the

costs and benefits of the traits associated with masculine and feminine faces in men differ in importance in different contexts, and women's preferences have evolved to vary in a calibrated way to these contextual cues (Little, DeBruine, & Jones, 2011).

In research supporting this theory, it has been found that women tend to prefer more masculine male faces when they are most fertile (Penton-Voak & Perrett, 2000; Penton-Voak et al., 1999), when they are in short-term rather than long-term mating contexts (Little, Jones, Penton-Voak, Burt, & Perrett, 2002; Penton-Voak et al.,

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1999), when they are oriented toward short-term rather than long-term mating (Burt et al., 2007; Waynforth, Delwadia, & Camm, 2005), when they see themselves as more attractive than average (Little, Burt, Penton-Voak, & Perrett, 2001), when they are exposed to pathogen cues (DeBruine, Jones, Crawford, et al., 2010; Little, Jones, & DeBruine, 2011), and when they are more sensitive to pathogen disgust (DeBruine, Jones, Tybur, et al., 2010). In other words, women display a stronger preference for masculine faces when genetic benefits can be reaped (in fertile phases of the menstrual cycle), when genetic benefits are the only fitness benefits on offer (as in short-term mating, when paternal investment is not on offer), when there is less need to make a trade-off (in more attractive women who may be able to attract and retain a mate with both good genes and good dad potential), and when genetic benefits (theorized to include higher immunocompetence) are relatively more important (i.e., in high-pathogen environments or in pathogen-sensitive individuals). In addition, the preferences of women who have been exposed to cues of resource scarcity (Little, Cohen, Jones, & Belsky, 2007) and women who perceive themselves as relatively low in socioeconomic status (Lee et al., 2013) tend more toward feminized male faces. These findings are consistent with a greater preference among women for facial femininity in men when paternal investment is more important.

This evolved-context-dependence account of women's preferences regarding masculinity had until recently been widely accepted (Roberts & Little, 2008), but in the past few years, it has been subject to intense debate. The logic of the underlying theory and the methods used to support it have been questioned (Scott, Clark, Boothroyd, & Penton-Voak, 2013), alternative explanations for key findings have been proposed (Brooks et al., 2010; but see DeBruine, Jones, Little, Crawford, & Welling, 2011; Moore et al., 2013; Scott et al., 2014), findings have been presented that are hard to reconcile with the theory (Lee et al., 2014; Lee & Zietsch, 2015; Scott et al., 2014), and conflicting meta-analysis results have cast some doubt on the idea that the fertility cycle has an effect on women's preferences (Gildersleeve, Haselton, & Fales, 2014; Wood, Kressel, Joshi, & Louie, 2014).

In the present study, we addressed the controversy from a different angle: We compared the relative magnitude of the context-dependent variation described earlier with the magnitude of genetic (heritable) variation in women's preferences regarding masculinity in male faces. It is unknown whether or to what extent genetic variation among women influences such preferences. Previous studies (Verweij, Burri, & Zietsch, 2012; Zietsch, Verweij, & Burri, 2012) have demonstrated heritable variation in various mate preferences, including preferences for specific sexually dimorphic physical traits (Verweij et al.,

2012), but preferences for different traits varied significantly in heritability (i.e., the proportion of variation due to genetic variation). Indeed, some traits were estimated to be not heritable at all, whereas others exhibited substantial heritability, up to 50%. The magnitude of context-dependent effects on women's preferences regarding facial masculinity is not well understood either, because the relevant studies have not usually employed large samples, which made their effect-size estimates imprecise. Consequently, we have no clear idea of how much of the variation in women's preferences regarding facial masculinity is likely to be genetic or how this compares with the variation attributable to context-dependent shifts. This knowledge is crucial in weighing the merits of the adaptive theory of context-dependent variation in preferences.

In the study reported here, we used a large sample ($N = 2{,}160$) of identical and nonidentical female Finnish twins and their siblings who were assessed for preferences regarding facial masculinity, menstrual-cycle information (for conception risk), sociosexuality (for orientation toward short-term relationships), self-rated attractiveness, and pathogen disgust sensitivity. We used a classical twin design to estimate the heritability of preferences regarding facial masculinity and to compare the magnitude of these effects with the magnitude of context-dependent effects.

Method

Participants

Participants were 2,160 female identical and nonidentical twins and their female siblings from 1,729 families in Finland (mean age = 33.11 years, *SD* = 5.00). This is a subsample of the population-based Genetics of Sexuality and Aggression twin sample. We targeted women who had participated in a similar data collection in 2005–2006 (described in Johansson et al., 2013) who had indicated an interest in participating in similar survey studies in the future. The new data were collected in the fall of 2013. All data were collected through a secure, online questionnaire. In total, we sent invitations to participate to 5,197 women by postal mail. Individuals who did not respond within 2 weeks were sent a reminder letter; another 2 weeks without a response led to a second reminder letter. Twenty-three individuals could not be reached (because the intended recipient had, e.g., moved abroad or passed away after the addresses were obtained from the Central Population Registry of Finland). In total, 2,249 women responded; of these, 73 did not wish to participate. Thus, the final response rate was 43.5%. The Ethics Committee of the Abo Akademi University (Turku, Finland) approved the research plan in accordance with

Fig. 1. An example stimulus from the masculinity preference measure. The face on the left is 50% masculinized, and the face on the right is 50% feminized.

the Helsinki Declaration. All participants provided written informed consent.

Materials and procedure

All measures were translated into Finnish, and a panel of four individuals with excellent command of both Finnish and English subsequently reviewed the translations. Participants completed the following measures as part of a larger online questionnaire on other topics.

Preference for facial masculinity. Preference for facial masculinity was measured using a standard forced-choice task, a well-established paradigm used in previous research (e.g., Perrett et al., 1998). Participants were shown two images of the same face side-by-side, but one image was manipulated to be more masculine, and the other was manipulated to be more feminine. Participants rated which face they found more attractive on an 8-point scale (1 = *left is much more attractive*, 8 = *right is much more attractive*). Participants were shown 21 pairs of faces presented in random order; the masculine face was also randomly presented on either the right or left side. Facial masculinity preference score was calculated as the mean across all trials after reverse scoring the relevant face pairings (α = .90). Note that we did not specify whether the face was being rated for attractiveness as a short-term or long-term partner, which is specified in some previous studies.

The facial images were males with neutral expressions from the FACES database (Ebner, Riediger, & Lindenberger, 2010), manipulated in the Psychomorph Online software package (DeBruine & Tiddeman, 2014). The age of the individual faces is not known, but we

chose older-looking faces from the "young" set (ages 19–31 years) of the FACES database so as to be similar to the average age of the twins. To manipulate face shape, we first created composite male and female faces from 25 individuals of each sex. The linear shape difference between the composite male and female face shapes was then computed on the basis of 129 landmarks. This difference, representing the sexual dimorphism dimension, was then applied to each male individual face at ±50% while keeping color and textural information of the original face constant. Effectively, this manipulated each face along the sexual dimorphism axis (either by increasing masculinity or femininity) while retaining the identity of each face. This methodology is standard and used in previous research investigating women's preferences regarding facial masculinity in men (for further detail, see Benson and Perrett, 1993; Perrett et al., 1998). For example faces, see Figure 1.

Sociosexual-Orientation Inventory. The Sociosexual-Orientation Inventory (Simpson & Gangestad, 1991) measures the willingness of participants to engage in uncommitted sexual relations. This measure includes items measuring behavioral sociosexuality (e.g., "With how many different partners have you had sex within the past year?") and items on attitudinal sociosexuality (e.g., "Sex without love is OK"). Scores for each item on the Sociosexual-Orientation Inventory were standardized, and outliers were Winsorized (±3 *SD*; 19 participants). Participants' sociosexuality scores were calculated as the mean of the standardized, Winsorized scores (α = .72).

Three-Domain Disgust Scale. On the Three-Domain Disgust Scale (Tybur, Lieberman, & Griskevicius, 2009),

participants are asked to rate the degree to which they find 21 statements disgusting (0 = *not disgusting at all*, 6 = *extremely disgusting*). Items measure disgust across three domains: pathogen disgust, moral disgust, and sexual disgust. In the current study, we focused on pathogen disgust, which refers to aversion to exposure to pathogen contagions that could threaten one's health and includes items such as "Sitting next to someone who has red sores on their arm" (α = .76).

Self-perceived attractiveness. Self-perceived attractiveness was measured using a single item previously used in Lukaszewski and Roney (2011). Participants completed the following sentence: "If you were to take a random sample of 100 other people from your area of your age and sex, you would be more physically attractive than ___% of them." This effectively measured participants' perceptions of their own attractiveness on a 100-point scale.

Conception risk. Participants' conception risk was estimated on the basis of a number of items regarding contraception use and menstrual cycle (for the items, see Supplemental Materials available online). These items collected information about whether hormonal contraceptives were used, whether hormonal contraceptives had been started or stopped in the past 2 months, the start date of the most recent menstrual cycle, the average or normal number of days between menses (menstrual cycle length), and the extent to which the menstrual cycle fluctuated from month to month.

We used four methods commonly reported in the literature to calculate conception-risk scores from self-report data. The four methods differ in (a) whether cycle day is calculated using the count-forward or count-back method and (b) whether conception risk is a dichotomous variable or a continuous variable. We report results using the count-forward method and conception risk as a continuous variable. Descriptions and results for the other methods are in the Supplemental Material. The count-forward method involved calculating cycle day by counting the number of days between the date women reported as the start of last menses and the date they completed the questionnaire. Continuous conception-risk percentage was estimated from cycle day according to the method described in Wilcox, Dunson, Weinberg, Trussell, and Baird (2001), which provides a conversion table of likelihood of conception according to cycle day given a single act of sexual intercourse. Following the method of previous studies, for the conception-risk analyses (Penton-Voak et al., 1999), we used only the subset of 574 women who were naturally cycling (i.e., not using

hormonal contraceptives) and had regular menstrual-cycle lengths.

Statistical analyses

In our statistical analyses, we applied full-information maximum-likelihood modeling procedures using the OpenMx software package (Boker et al., 2011), which accounts for the nonindependence of twin pairs. In maximum-likelihood modeling, a model's goodness of fit to the observed data follows a χ^2 distribution. By comparing the change in χ^2 with the change in degrees of freedom, one can test whether dropping or equating specific model parameters (e.g., the correlations for identical and nonidentical twin pairs) significantly worsens the model fit. We tested hypotheses regarding model parameters in this way.

Identical twins share all of their genes, whereas non-identical twins and siblings share on average half of their segregating genes; consequently, if genetic influences play a role, identical and nonidentical pairs would be expected to show different degrees of within-pair similarity in a trait. We used structural equation modeling to partition the variation in facial-masculinity preference into additive genetic (*A*), nonadditive genetic (*D*), and residual (*E*) sources. Additive genetic variation refers to the sum of allelic effects within and across genes. If additive genetic variation were the sole source of variation in preferences, we would expect correlations of 1.0 for identical twins and .5 for nonidentical twins. Nonadditive genetic variation refers to genetic effects due to dominance and epistasis (allelic interactions within and between genes, respectively). If dominant genetic variation were the sole source of variation in preferences, we would expect correlations of 1.0 for identical-twin pairs and .25 for non-identical-twin pairs; epistatic variation would predict lower correlation in nonidentical-twin pairs but is nevertheless captured by the *D* estimate. Residual variation refers to variance unexplained by the model and can include measurement error and idiosyncratic environmental influences; these factors cause no similarity in either identical or nonidentical twins. Variation as a result of the twin pairs' shared environment (*C*) can be estimated using twin-sibling data but not concurrently with *D*. Data indicating that nonidentical twins are less than half as similar as identical twins (as is the case in the current study) suggest that *D* effects are greater than *C* effects, and so it is standard practice to model *D* instead of *C* (Neale & Cardon, 1992; Posthuma et al., 2003).

As is standard for twin-family designs, we used maximum-likelihood modeling, which determines the combination of *A, D,* and *E* that best fits the observed twin-pair correlations. See Posthuma et al. (2003) for further detail

Table 1. Twin- and Sibling-Pair Correlations for Women's Preferences Regarding Men's Facial Masculinity

Group	r
Identical twins (*n* = 131 pairs)	.38 [.22, .54]
Nonidentical twins (*n* = 100 pairs)	.10 [–.10, .30]
Siblings (*n* = 248 pairs)	.13 [.00, .25]
Nonidentical twins and siblings (*n* = 348 pairs)	.11 [.01, .22]

Note: Values in brackets are 95% confidence intervals.

on the classical twin design and analyses. We used bivariate models in Mx to assess the phenotypic (observed) correlation between each context-dependent variable and women's facial-masculinity preferences. The difference between these models and a standard Pearson correlation is that Mx family relatedness is modeled and thus accounted for, which prevents the bias in p values that would otherwise result from the nonindependence of observations. In addition, we included age as a covariate in all analyses, effectively partialling out any effects of participant age on facial masculinity preference and its associations with contextual variables.

Results

Preliminary analyses

Overall, mean preference for male facial masculinity was 5.26 (*SD* = 0.89), which indicates that there was a slight but significant overall preference, $t(2159) = 39.64$, $p < .001$, for facial masculinity (midpoint = 4.5). Mean facial-masculinity preferences did not significantly differ between identical and nonidentical twins, $\chi^2(1) = 2.70$, $p = .10$, or between twins and siblings, $\chi^2(1) = 0.02$, $p = .88$, which suggests nothing unusual about identical twins' preferences, or those of twins in general, compared with nontwins. The preference correlations of nonidentical twin pairs and sibling pairs did not differ significantly, $\chi^2(1) = 0.05$, $p = .82$, which was expected given their equivalent genetic association and our assumption of equally similar environmental influences;

therefore, nonidentical twin and sibling correlations were equated in subsequent modeling.

Genetic analysis

Twin-pair correlations are reported in Table 1. The correlation for identical twins was significantly greater than for nonidentical twins and siblings, $\chi^2(1) = 8.55$, $p = .003$, which suggests a genetic influence on women's facial-masculinity preferences.

Using biometric modeling (Table 2), we estimated that 38% of the total variance in women's facial-masculinity preferences could be explained by additive and nonadditive genetic variation (*A* + *D*). Table 2 also provides estimates from a model that assumes all the genetic variation is additive (*AE* model); in that case, the genetic component of variation was estimated a little lower, at 33%.

These data indicate an alternative explanation of the heritability of women's facial-masculinity: Because there was a mean preference for masculinized faces, the between-individual variation may partly reflect strength of preference for masculine faces ("choosiness") rather than direction of preference toward masculine versus feminine faces. To address this possibility, we ran the modeling again using dichotomized face preferences—that is, for each face pair, we coded preferences as 0 (feminized face preferred) or 1 (masculinized face preferred). This analysis revealed a slightly higher heritability (42%), which indicates that the genetic influence cannot be explained by genetic variation in choosiness (Table 2).

Context-dependent shifts

To compare the magnitude of genetic effects with the magnitude of context-dependent shifts, we assessed the association between participants' facial-masculinity preferences and their scores for sociosexual orientation, pathogen disgust, self-perceived attractiveness, and conception risk (Table 3). As in previous research, there was a significant positive correlation between sociosexual-orientation score and facial-masculinity preference, but the

Table 2. Proportion of Variance in Women's Preferences Regarding Men's Facial Masculinity Accounted for by Additive Genetic (*A*), Nonadditive Genetic (*D*), and Residual (*E*) Effects

Model	A	D	A + D	E
Preference as a continuous variable				
ADE model	.07 [.00, .42]	.31 [.00, .50]	.38 [.24, .50]	.62 [.50, .76]
AE model	.33 [.21, .44]	—	—	.67 [.56, .79]
Preference as a dichotomous variable				
ADE model	.00 [.00, .37]	.42 [.00, .53]	.42 [.29, .53]	.58 [.47, .71]
AE model	.35 [.22, .47]	—	—	.64 [.53, .78]

Note: Values in brackets are 95% confidence intervals.

Table 3. Phenotypic Correlations Between Women's Preferences Regarding Men's Facial Masculinity and Contextual Variables

Contextual variable	n	r
Sociosexuality	2,160	.07 [.03, .11]
Pathogen disgust	2,160	−.01 [−.05, .03]
Self-rated physical attractiveness	2,160	.03 [−.01, .08]
Conception risk	590	−.08 [−.16, .01]

Note: Values in brackets are 95% confidence intervals.

effect size was very small. Contrary to previous research, there was no significant association between either pathogen disgust or self-perceived attractiveness and facial-masculinity preference. For conception risk, regardless of the method used to calculate the score, we found a trend toward negative association (and in one case a significant negative association) with facial-masculinity preference, such that women with higher conception-risk scores preferred greater facial femininity. The direction of this association was opposite that expected on the basis of previous findings. Overall, these previously identified context-dependent effects (excluding conception risk, which was opposite that expected from predictions) explained less than 1% of the variation in women's preferences regarding facial masculinity, and genetic factors explained 38% of the variation.

Discussion

In the present study, we aimed to estimate the magnitude of genetic variation in women's facial-masculinity preferences and compare it with the magnitude of variation accounted for by several previously established context-dependent factors. The results were clear: The variation accounted for by genes (38%) was vastly greater than the variation accounted for by the combined effects of the measured context-dependent factors (< 1%).

This is the first research to test for genetic variation in women's facial-masculinity preferences. Previous work emphasized the role of the environment, mostly via context dependence of potentially adaptive origin, but also recently via "visual diet" (i.e., the types of faces encountered in one's social environment; Scott et al., 2014). Prior genetic research on preferences for several other sexually dimorphic physical features (Verweij et al., 2012) showed a wide range of heritabilities, including zero, so there was no clear prior expectation as to the presence or magnitude of genetic effects on women's facial-masculinity preferences. The demonstration that genetic differences between individual women were responsible for a large proportion of the variance in their facial-masculinity preferences is therefore a significant advance in understanding. The

advance is reinforced by our findings regarding the relative size of the context-dependent variables that we investigated simultaneously. Because of the size of our sample, we were able to estimate with unusual precision the size of several context-dependent effects; invariably, these effect sizes were very small ($R^2 < .01$) and had narrow confidence intervals. The widest confidence intervals were for the effect of menstrual cycle (as a result of the reduction in sample size produced when we excluded users of hormonal contraceptives).

Although there was low power (36%) to detect a very small positive effect of fertility (Hedges's $g = .13$, as estimated in the meta-analysis by Gildersleeve et al., 2014), the fact that our nonsignificant effect was in the opposite direction allows us to remain confident that any positive effect is very small indeed (upper 95% confidence limit for $r = .01$). This finding is consistent with those from other large recent studies that have failed to replicate earlier findings of a menstrual-cycle effect on women's facial-masculinity preferences (e.g., Harris, 2011; Muñoz-Reyes et al., 2014; Scott et al., 2014). For the other variables, we had 99% power to detect effect sizes found in previous studies (DeBruine, Jones, Tybur, et al., 2010; Little et al., 2001; Waynforth et al., 2005). Only sociosexual orientation showed a significant effect consistent with previous research (Little et al., 2002), but it was very small ($R^2 = .005$). Overall, our results suggest that any context-dependent effects are much smaller and less robust than previously thought.

The results also call into question the evolutionary significance of these context-dependent effects, because selection would be expected to deplete genetic variation (Fisher, 1930) and to strengthen any adaptive context-dependent effects. It is unclear, then, why the context-dependent effects are so minuscule against the background of large genetic effects. An alternative possibility is that the context-dependent effects on women's facial-masculinity preferences are not the result of direct selection. For example, women's menstrual cycles involve great fluctuations in sex hormone levels, which aid the production of eggs and the preparation of the uterus for pregnancy. However, sex hormones have wide-ranging effects, so their fluctuation across the menstrual cycle can cause additional changes, such as complex mood effects (Kiesner, 2011) and increased risk of migraine (Brandes, 2006). These additional effects, and potentially mate-preference effects, could be side effects rather than being tailored by selection to optimize behavior at different times in the cycle. If so, it would not be surprising that the effects are small.

Regarding our lack of replication of the positive association between women's pathogen disgust sensitivity and masculinity preferences, a possibility is that the age of our sample ($M = 33.1$ years) and target faces

(~30 years) could have masked the effect: It has been suggested that this effect is specific to young adults rating young faces (Lee & Zietsch, 2015). Furthermore, given our lack of replication and the small size of all the measured context-dependent effects, note that (a) the imperfect reliability of the contextual measures reduces the variance they can account for, and (b) we measured only a few of the many possible contextual factors that could be important. Consequently, we do not intend to dismiss contextual influences on women's facial-masculinity preferences as a worthwhile avenue of investigation; most of the preference variation is still unaccounted for by genetic variation, leaving plenty of scope for true environmental influences, whether they are adaptive or not. We do, however, emphasize the previously unrealized importance of genetic variation in causing preference variation, and the challenge now is to clarify how this fits or conflicts with adaptive (e.g., facultative) explanations. For example, a facultative response that is contingent on a heritable trait will exhibit heritability itself (termed *reactive heritability*), meaning that genetic variation in women's facial-masculinity preferences could in principle reflect facultative processes. Note, however, that this is not substantively relevant with respect to the individual-difference variables investigated here because the phenotypic correlations were so small or absent.

A limitation of our study, inherent to the classical twin design, is that there is little power to distinguish additive from nonadditive genetic effects, and estimates of such differences are subject to bias (Keller, Medland, & Duncan, 2010). However, the estimate of the total (additive plus nonadditive) genetic effect has been shown to be relatively unaffected by these biases (Keller et al., 2010), so it is this estimate to which we pay most attention. In addition, mathematical modeling has shown that in highly polygenic traits, nonadditive genetic variance is likely to be small relative to additive variance (Mäki-Tanila & Hill, 2014), so our high estimate of the nonadditive component of genetic variance should be treated with caution. Extended twin-family designs (e.g., including twins' spouses and parents) afford more power to detect nonadditive genetic effects with much less bias and would be a fruitful avenue for future research.

Perhaps more important is obtaining genetically informative data on both men's and women's preferences regarding opposite-sex facial masculinity as well as their own facial masculinity. Such data would enable tests of whether intersexual selection is involved in the evolution of facial sexual dimorphism, which is an unresolved and controversial issue in the field (Scott et al., 2013). Mate-selection models predict positive cross-sex genetic correlation between preference and preferred trait (Fuller, Houle, & Travis, 2005; Lande, 1981). Such models would

predict, in opposite-sex twin pairs, positive genetic correlation between sisters' preferences regarding male facial masculinity and their brothers' facial masculinity (if female choice plays a role in facial sexual dimorphism), or positive genetic correlation between brothers' preferences regarding female facial femininity and their sisters' facial femininity (if male choice plays a role in facial sexual dimorphism).

Overall, our findings demonstrate the importance of genetic differences in explaining variation in women's preferences regarding male facial masculinity while casting doubt on the importance of the particular context-dependent effects that have dominated research and theory on the topic until now. This may suggest a refocusing in the field toward understanding the wide genetic variation in these preferences and how this variation relates to the evolution of facial sexual dimorphism.

Author Contributions

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Declaration of Conflicting Interests

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Supplemental Material

Additional supporting information can be found at http://pss .sagepub.com/content/by/supplemental-data

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