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Personality and testosterone in men from a high-fertility population

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ABSTRACT

Extraversion, a personality dimension associated with sociability, activity and dominance, predicts a man's mating effort in various human populations. At a proximate level, individual differences in extraversion are likely to be mediated through testosterone, a strong hormonal correlate of men's reproductive effort. However, the rare attempts to address this question have all been conducted in populations with low-fertility schedules, thus limiting the generality of the results. Using demographic, questionnaire and hormonal data from a high-fertility polygynous human population of Senegal, we first show that extraversion, a personality dimension predicting men's mating behavior in this population, is associated with inter-individual differences in testosterone profiles, with men in the top quartile of extraversion distribution having 29% higher testosterone levels. We then show that personality profiles for neuroticism, openness and agreeableness are independent from testosterone levels. Since extraversion is the only personality dimension predicting men's mating and reproductive success in this population, we suggest that variation in testosterone levels is primarily relevant for personality traits related to reproductive effort. The results have further implications to discuss possible evolutionary scenarios for the maintenance of variation in personality traits.

1. Introduction

Personality traits, defined as stable individual behavioral dispositions, predict male reproductive success in various non-human species. For instance, bold individuals (i.e. those displaying high-risk behaviors) gain more offspring, but boldness also incurs survival costs (Smith & Blumstein, 2008). In humans, boldness has been linked with extraversion (Gosling, 2001), a personality dimension positively related to pro-social behavior which reflects sociability, assertiveness, activity, dominance and positive emotions (McCrae & John, 1992). There is now some evidence that extraversion predicts men's mating effort and long term mating success. For example, extraverted male college students score higher on sociosexuality and are more likely to pursue short-term mating cross-culturally (Schmitt, 2008). This is consistent with long term mating dynamics in both modern and traditional human populations, where extraversion positively predicts men's mating success, including higher number of lifetime sexual partners and frequency of extra-pair copulations (Nettle, 2005) as well as a higher probability of polygyny (Alvergne, Jokela, & Lummaa, 2010). Such increased mating effort and success are ultimately translated into a higher number of children among extraverted men in such population where the use of modern contraception remains limited (Alvergne et al., 2010).

In species with paternal care towards the offspring, male mating effort is balanced against parenting effort. This trade-off is regulated through testosterone in a wide range of species including humans (Alvergne, Faurie, & Raymond, 2009; Gray, Ellison, & Campbell, 2007; McGlothlin, Jawor, & Ketterson, 2007; Muller, Marlowe, Bugumba, & Ellison, 2009), with high levels of testosterone predicting high investment in mating effort. Consequently, male behavioral profiles involved in mating effort in humans (e.g. high score on the extraversion dimension) are also expected to be proximally regulated through testosterone. In line with this, it has been shown that testosterone levels positively predict psychological factors related to the dominant facet of extraversion (e.g. sensation-seeking (Campbell et al., in press; Daitzman & Zuckerman, 1980), but see (Kerschbaum, Ruemer, Weisshuhn, & Klimesch, 2006; Rosenblitt, Soler, Johnson, & Quadagno, 2001)), as well as to the friendship facet of extraversion (e.g. sociability (Daitzman & Zuckerman, 1980)). More directly, one previous study based on 40 white unmarried male subjects aged 17–20 years old from US suggested that extraversion positively correlates with variation in testosterone levels ($r = 0.41$, (Daitzman & Zuckerman, 1980)). However, the interpretation of the link between testosterone and extraversion is complicated by the sample studied. First,

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individuals were college students and are thus not always representative of the general population of reproductive males. Second, they were preselected on the basis of either high or low scores on disinhibition (a subscale of the Sensation-Seeking Scale), thus limiting the investigation to individuals with extreme personality profiles. Finally, this previous study, as well as the previous indirect ones mentioned above, has been conducted in a modern environment with non-natural fertility, thus limiting the understanding of the role of ecological factors and thus the generalization of the results. Consequently, our understanding of the proximate mechanisms giving rise to between-male differences in both personality and mating vs. parenting effort remains incomplete.

We investigate the relationship between testosterone and personality variation in men from a high-fertility, polygynous Senegalese population. This population of subtraditional agriculturalists, characterized by a relatively homogenous socio-economic environment (as compared to modern populations), presents several advantages. First, the competition between males that results from the polygynous mating system translates into large differences in reproductive success. Second, inter-individual differences in testosterone have previously been shown to predict men's mating effort in the same population (Alvergne et al., 2009). Finally, the link between personality and reproductive success has already been established, with personality assessed using the most widely acknowledged model of personality (i.e. Big-Five factor model (McCrae & John, 1992)): while high extraversion in this population positively predicts men's mating success, other measured personality traits (neuroticism, agreeableness, openness) do not (Alvergne et al., 2010). Following current knowledge on the evolved function of testosterone, i.e. regulating male mating effort, we hypothesize variation in testosterone levels to predict inter-individual differences in the personality dimensions that predict mating success in the studied population.

2. Methods

2.1. Study population

The study was conducted in traditional villages in rural Senegal. The most frequent ethnic groups in this area are the Sereer and the Wolof. The population is agricultural with both subsistence and cash crops and characterized by patrilocality and patrilineal inheritance, with polygynous marriages allowed. Recruitment of families and data collection were approved by both the French National Committee of Information and Liberty and the ethical committee of the Senegalese National Research Council for Health, and informed consent was obtained from all participants. We recruited a total of 41 men, all fathers, from four villages and with age averaging 41.0 years (30–51). Selection of both the villages and the men was random (although dependent on the willingness of families to participate), and for one village, all resident men were included, so our sample is likely representative of the larger community.

2.2. Demographic and anthropometric data

To investigate the underlying pathways through which personality could be related to testosterone (T) levels and to control for any confounding effects on hormonal levels and personality, we collected information on men's age, body condition (body mass index = weight (kg)/height^2 (cm)), marital status (i.e. monogamous, $N = 27$ or polygynous, $N = 14$), number of children, birth order and social status. Social status was classified based on the type of house: either modern, made with expensive material and resistant to several rainy seasons (high social status, $N = 16$), or traditional, made with cheaper material and resistant to fewer rainy seasons (low social status $N = 25$). Note that while this variable is positively correlated with land possessions (Alvergne et al., 2010), it is likely to be more general as it refers to resources obtained from various activities (i.e. not only from agriculture).

2.3. Personality assessment

Personality was assessed using an adapted version of the international Big-Five mini-markers questionnaire, informing on the five personality dimensions, i.e., extraversion (E), agreeableness (A), neuroticism (N), openness (O) and conscientiousness (C) (Thompson 2008). Such self-reports correlate well with objective measures of behavior (McCrae & Costa, 1987) and are stable over time, in line with a literature on personality suggesting that it has heritable genetic basis (Bouchard, 1994) with only modest degree of changes across the life course. For example, while the mean level of personality changes from adolescence to adulthood (i.e. decreases in neuroticism, extraversion, and openness and increases in agreeableness and conscientiousness from adolescence to adulthood), there are only few changes in all five domains of personality after age 30, when individual differences in personality traits become fixed (McCrae & Costa, 1994). While data on the development of behavior from African populations are, to our knowledge, currently unavailable, such a developmental pattern appears to be cross-culturally consistent (McCrae, 2009, June).

Originally composed of 40 items, the questionnaire was reduced to 27 adjectives after assessment of the functional and conceptual equivalence of the adjectives in the Senegalese culture in order to keep the questionnaire short to maintain participant interest. Interviews were conducted in privacy between each participant and the researcher. The questionnaire was translated into the local language by linguists specialized in the local languages and played using a voice recorder. The participants were told to describe how much each adjective described their personality on a scale ranging from 0 to 3 (0: not at all; 1: a little bit; 2: a lot, 3: perfectly). Based on α-Cronbach coefficients, only questions maximizing the internal reliability of each dimension (α-Cronbach > 0.5) were kept to build personality variables (see Alvergne et al., 2010 for values). Concerning conscientiousness, however, more than 90% of data points were biased towards the highest value, probably due to strong cultural enforcement; therefore this dimension was not included in the analysis. The reliability of the other personality traits obtained did not differ from those usually found in Africa (E: .55; A: .62; N: .63; O: .58, Schmitt, Allik, McCrae, & Benet-Martínez, 2007). All dimensions were independent from each other (all $|r| < 0.20$) and of age (all $|r| < 0.15$).

2.4. Hormonal data

2.4.1. Sample collection

T levels were measured from saliva. This non-invasive technique has previously been validated and yields T levels that are highly correlated with the biologically active fraction of T in the serum (Ellison, 1988; Read, 1993). Men provided morning samples on two consecutive days: morning levels have been previously related to male mating effort in this population (Alvergne et al., 2009). Participants were asked to rinse their mouth with water 5 min before providing saliva. The time of collection (8–11 am) was not correlated with T levels (day 1: Pearson's correlation, $r = -0.11$, df = 33, $P = 0.52$; day 2: $r = 0.18$, df = 33, $P = 0.29$).

2.4.2. Assessment of T levels

T levels in saliva were determined by Luminescence Immuno Assay (LIA) technique, using LIA Testosterone kits (IBL, Hamburg; see Alvergne et al., 2009 for details). The two saliva samples of each participant were run in duplicate and had a mean intra-assay coef-

ficient of variation (CV) of 6.24% ± 3.24. Inter-assay CV for T measurements were 23% for low controls and 11% for high controls. The morning T levels measured for the first and second day were significantly correlated (Pearson's correlation, $r = 0.69$, df = 33, $P < 0.001$). The variable used for statistical analysis corresponds to the mean morning T levels obtained on day 1 and 2 (mean ± SD = 60.8 ± 28.5 pg/ml).

2.5. Statistical analyses

We used mixed effects models to control for inclusion of four villages in our study. We first investigated the effects of potential confounding variables (i.e. age, ethnical group, BMI, birth order and social status) to explain variation in both T levels and personality dimensions. T levels were normalized using a log-transformation. Second, we investigated whether inter-individual differences in personality are predicted by variation in T levels, controlling for variables that were found confounding in the first place. When the response was modeled as Gaussian (T levels), *P*-values were obtained using *F*-tests. For Poisson distributions (i.e. for personality traits), *P*-values, estimates and confidence intervals were calculated from posterior distribution of the parameters generated by mixed models (Bates & Sarkar, 2007). Analyses were carried out with R.2.4.1.

3. Results

We found evidence that variation in testosterone levels in men predicts inter-individual differences in personality only for the dimension associated with mating success in this population. T positively predicted extraversion ($\beta = 0.56$; 95% CI [0.07;1.06], $P = 0.03$, Fig. 1a), a dimension previously found to be associated with marital status (monogamous vs. polygamous) for the same men (Alvergne et al., 2010). T concentrations were 29% higher in men from the top quartile of the extraversion dimension (mean ± SD = 64.87 ± 1.48) than in men from the lower quartile (45.80 ± 1.44). Overall, T levels alone accounts for 15.2% of the variance in extraversion. Other personality traits not related to mating success were not significantly related to variation in T levels (i.e. neuroticism ($\beta = 0.08$; 95% CI [−0.33;0.51], $P = 0.68$, Fig. 1b); agreeableness ($\beta = -0.03$; 95% CI [0.45;3.62], $P = 0.87$, Fig. 1c) and openness ($\beta = 0.04$; 95% CI [−0.38;0.46], $P = 0.84$, Fig. 1d). These analyses are controlled for age, which negatively predicts testosterone levels ($\beta \pm SD = -0.04 \pm 0.02$, $F_{1,23} = 5.61$, $P = 0.03$). The findings are not confounded by either birth order, body mass index, ethnical group or social status, all independent from testosterone levels ($P = 0.49$; $P = 0.67$; $P = 0.24$; $P = 0.42$, respectively).

4. Discussion

We first found that extraversion, a personality dimension reflecting a sociable, outgoing, risk-taking, and dominant behavioral disposition, is positively associated with testosterone levels in men from a high-fertility polygynous population. These results replicate those obtained in a low-fertility population using a sample of college students for which testosterone levels were found to be higher in extraverted individuals (Daitzman & Zuckerman, 1980). This suggests that similar proximate mechanisms are responsible for variation in extraversion across human populations. Secondly, testosterone levels were not found to

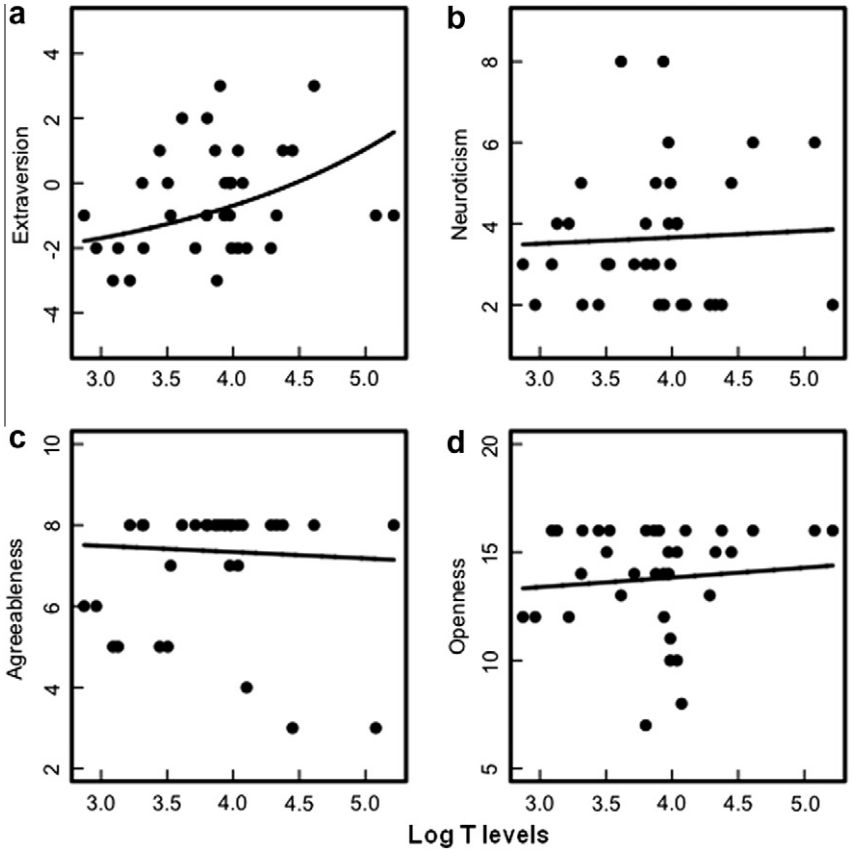

Fig. 1. Testosterone and personality dimensions. (a) extraversion, (b) neuroticism, (c) agreeableness, (d) openness. The log of testosterone levels (mean of two morning samples) is regressed against each personality dimension. Raw data are indicated by dots and plain lines correspond to fitted relationships. A positive correlation between testosterone and personality is observed for the extraversion dimension.

predict inter-individual differences in neuroticism, openness and agreeableness. Since extraversion is the only personality dimension predicting mating success and subsequent fitness in this population (Alvergne et al., 2010), these results support the hypothesis according to which male behavioral profiles involved in mating effort in humans (e.g. high score on the extraversion dimension) are expected to be proximally regulated through testosterone.

Since extraversion is a personality dimension partly reflecting dominance, it is possible that the higher testosterone levels observed for extraverted men result from higher dominance levels in those men. Indeed, there is now considerable evidence that dominance is regulated through testosterone variation in a wide range of species (Wingfeld, Hegner, Dufty, & Ball, 1990), including humans (Mazur & Booth, 1998). Measures of sensation-seeking behavior, generally predicted by dominance profiles (Demaree, DeDonno, Burns, Feldman, & Everhart, 2009), would help to validate this possibility. One could also argue that differences in men's extraversion result from variable exposure to prenatal testosterone, rather than variation in adulthood testosterone levels. Indeed, it has been proposed that sex-related exposure to testosterone *in utero* could lead to sex-related profiles of personality in adulthood (Fink, Manning, & Neave, 2004). However, the link between the second-to-fourth digit ratio, a proxy for exposure to prenatal testosterone, and the Big-Five personality dimensions has received mixed evidence to date, and prenatal exposure to testosterone has not been found to predict inter-individual differences in men's extraversion (Fink et al., 2004; Luxen & Buunk, 2005).

We found that personality profiles for neuroticism, agreeableness and openness to experience were not predicted by variation in testosterone levels. Interestingly, in the studied population, these personality traits were not related to mating behavior either. Building on these results, we propose that variation in personality will be predicted by T levels only for dimensions that are related to men's mating success in a given socio-ecological environment. However, depending on the socio-cultural context, resource acquisition and subsequent mating access might be optimized for different dimensions, or, within a given dimension, for different values or sub-dimensions. We would thus recommend investigating the relationship between personality and reproductive success when assessing the link between testosterone and personality. It is however worthy of note that although comparable to other studies conducted in African populations (Section 2), the reliability of personality dimensions obtained in this study is generally low, which precludes detecting small effects. Moreover, questionnaire data are sensible to noise resulting from cultural norms, and for instance, our measure of agreeableness is more likely to reflect cultural enforcement of high levels of cooperation (i.e. most data points correspond to the highest value) than inter-individual differences, so it is unclear whether or not agreeableness is related to T levels. Note that the impact of culture seems to be less important for extraversion, this dimension showing considerably more variation (see Fig. 1). Future studies using direct observations might nevertheless help to refine conclusions on the physiological correlates of inter-individual differences in personality.

Personality research has recently undergone a surge of interest from behavioral ecologists, and there is now strong evidence that inter-individual differences in temperament are associated with differential reproduction among individuals both in non-human animals (see Smith & Blumstein, 2008 for review) and humans (Alvergne et al., 2010; Eaves, Martin, Heath, Hewitt, & Neale, 1990; Jokela & Keltikangas-Jarvinen, 2009; Jokela, Kivimaki, Elovainio, & Keltikangas-Jarvinen, 2009; Nettle, 2006). The evolutionary forces involved in creating and maintaining personality variation are however still debated (Reale, Reader, Sol, McDougall, & Dingemanse, 2007). The present association between extraversion and testosterone in men suggests that variation in extraversion partly results from differences in men's reproductive strategies (i.e. relative investment in mating vs. investment effort) in the population. This supports the trade-off hypothesis according to which variation in personality can be maintained if personality traits are linked with life-history traits (Biro & Stamps, 2008; Nettle, 2005). More generally, research on the proximate mechanisms underlying personality variation might help testing competing scenarios.

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