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Integrating molecular genetics and evolutionary psychology: Sexual jealousy and the androgen receptor (AR) gene

David M.G. Lewis [a,*], Laith Al-Shawaf [b,c], Mareike C. Janiak [d], Sarah P. Akunebu [e]

[a] Murdoch University, Australia
[b] Bilkent University, Turkey
[c] Institute for Advanced Study, Berlin, Germany
[d] Rutgers University, United States
[e] St. Edward's University, United States

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ABSTRACT

Integrating evolutionary psychological and molecular genetic research may increase our knowledge of the psychological correlates of specific genes, as well as enhance evolutionary psychology's ability to explain individual differences. We tested the hypothesis that men's sexual jealousy mechanisms functionally calibrate their psychological output according to genetic variation at the androgen receptor locus. Mated men ($N = 103$) provided buccal cell samples for genotype fragment analysis and completed inventories assessing their sexually jealous cognitions and emotions. Results indicated that men with longer sequences of CAG codon repeats at the androgen receptor locus were more likely to perceive ambiguous social and environmental cues as indicative of their mates' infidelity, and experienced greater emotional upset in response to these cues. These results contribute to a growing body of research linking polymorphism at the AR locus to individual differences in psychology, and, to our knowledge, provide the first evidence pointing toward the heritability of sexual jealousy. Our discussion centers on whether the heritability of psychological differences implies direct genetic influences on the neurobiological substrate, or reflects functionally calibrated output from sex-typical and species-typical mechanisms. We conclude by describing how future research can more clearly differentiate between these alternative genetic models.

Evolutionary psychologists assert that identifying the genetic basis of a psychological phenomenon is not necessary to establish that the phenomenon under investigation is the output of an evolved psychological mechanism (see Confer et al., 2010; Lewis, Al-Shawaf, Conroy-Beam, Asao, & Buss, in press; Williams, 1966). Indeed, the location of a particular allele in the molecular genetic substrate is not relevant to establishing adaptation. Rather, to show that a psychological phenomenon is the output of an evolved adaptation, one must demonstrate specialized functional design (Cosmides & Tooby, 1997; Lewis et al., in press; Williams, 1966).

This does not imply that molecular genetics cannot valuably inform evolutionary psychology. If there are compelling theoretical reasons to believe that evolved psychological mechanisms are designed to be sensitive to the downstream products of specific genetic loci, then integrating evolutionary psychological and molecular genetic research could enhance both 1) our understanding of the psychological correlates of those genes and 2) evolutionary psychology's explanatory power at the level of individual differences in addition to sex-typical and species-typical psychological phenomena.

This paper aims to theoretically illustrate and empirically demonstrate the mutually informative potential of molecular genetics and evolutionary psychology. Specifically, the current study applied an evolutionary psychological framework to investigate individual differences in men's sexual jealousy as a function of genetic variation at the human androgen receptor locus.

1. Sexual jealousy

Ancestral men whose long-term mates were sexually unfaithful would have incurred substantial reproductive fitness costs. These include the staggering costs associated with being cuckolded and unwittingly investing in the offspring of another male, as well as the social costs of reputational damage (Buss, 2000). Selection would therefore have strongly favored the evolution of anti-infidelity adaptations in men.

Several theorists have proposed that sexual jealousy represents a coordinated suite of psychological processes designed to prevent mate defection and infidelity. Consistent with this proposal, the cognitive and

* Corresponding author at: Murdoch University, School of Psychology and Exercise Science, 90 South Street, Murdoch, Western Australia 6150, Australia.
E-mail address: d.lewis@murdoch.edu.au (D.M.G. Lewis).

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affective facets of sexual jealousy exhibit evidence of design to promote one's mate's fidelity (Buss, 2002). This includes triggering information-gathering about infidelity threat (Goetz, Shackelford, Romero, Kaighobadi, & Miner, 2008; Schützwohl, 2008) and producing negative emotions in response to one's mate's social interactions – in particular with potential mate poachers (Buss, 2000). Moreover, these affective states can motivate controlling behaviors or aggressive responses (Daly, Wilson, & Weghorst, 1982) to fend off these same-sex rivals and combat other threats to the relationship (Buss, 2000; Buss, Larsen, Westen, & Semmelroth, 1992; Daly et al., 1982; Symons, 1979).

2. Evolved individual differences

A condition-dependent individual differences model (e.g., Lewis, 2015; Lukaszewski & Roney, 2011; Tooby & Cosmides, 1990; Wolf, van Doorn, Leimar, & Weissing, 2007) posits that species-typical evolved psychological mechanisms are designed to process, as input, cues ancestrally predictive of the cost-benefit tradeoffs of alternative interpersonal strategies, and produce, as output, the psychological strategy of greater probabilistic net benefit for the individual, given his or her condition (Buss & Greiling, 1999; Nettle, 2006; Wolf et al., 2007).

The output of humans' psychological mechanisms is expected to be largely the same when 1) all individuals face the same adaptive problems (Buss, 1995), 2) these adaptive problems pose similar costs to all individuals, and 3) all individuals face these adaptive problems to the same degree. However, when individuals differ in *any* of these dimensions – such as when men differentially face the risk of their mates' infidelity – we should expect the output of their shared, evolved psychological mechanisms to diverge in systematic, functional ways.

3. Individual differences in infidelity threat

An exploration of evolved female mating strategies reveals why ancestral men would have faced differential likelihoods of being cuckolded. Women's reproductive success would have been enhanced when they were able to produce genetically robust offspring and secure long-term investment from their mates. To produce offspring of high genetic quality, a woman had to copulate with a man of high genetic quality. Yet, because desirable, high genetic quality men could have increased their own reproductive success by engaging in uncommitted mating with multiple women, selection would have favored the pursuit of short-term mating strategies among these men (Gangestad & Simpson, 2000). Indeed, physically attractive men of high genetic quality are precisely those men who are least monogamous and most likely to be sexually unfaithful (e.g., see Al-Shawaf, Lewis, & Buss, 2015; Buss, 2003; Gangestad & Thornhill, 2008). Consequently, women face tradeoffs in their mate selection: they may not always have been able to reliably secure both "good genes" and long-term investment from the same man (Gangestad & Simpson, 2000). This dilemma creates the background selective conditions for the evolution of a dual female mating strategy of 1) long-term mating with men willing to commit resources and investment and 2) seeking men of high genetic quality for short-term sexual relations (Gangestad & Simpson, 2000).

Because ancestral women could not have directly observed men's genes, their detection of men's underlying genetic quality had to have been indirect – based on observable cues. Because androgens have immunosuppressive effects, androgenization may be a costly signal indicating high genetic quality (Evans, Goldsmith, & Norris, 2000; Peters, 2000; Rantala, Vainikka, & Kortet, 2003; Zahavi, 1975). Selection may thus have favored a female preference for androgenized men as short-term mating partners (see Gangestad & Simpson, 2000; Gangestad & Thornhill, 1997; Penton-Voak et al., 1999). Empirical data support this hypothesis. Evidence suggests that women prefer short-term mates who exhibit above-average levels of a wide variety of characteristics associated with androgenization, androgenization, ranging from low vocal frequencies (see Feinberg et al., 2006) to a v-shaped torso (Hughes & Gallup, 2003).

An ancestral woman could have reaped both genetic and non-genetic benefits from engaging in a sexual affair (see Greiling & Buss, 2000), but she also could have incurred substantial costs from engaging in such liaisons. If she engaged in such an affair and was discovered, she could have lost her long-term partner, suffered reputational damage, and seen a decrease in her probability of securing future long-term mates (Forstmeier, Martin, Bolund, Schielzeith, & Kempenaers, 2011; Greiling & Buss, 2000). Selection would thus have favored extra-pair mating mechanisms in women that were only activated under conditions in which the probabilistic benefits outweighed the probabilistic costs.

The benefits of an extra-pair copulation with a man of high genetic quality would have depended on the genetic makeup of the woman's current long-term mate (Gangestad, Thornhill, & Garver-Apgar, 2005; Haselton & Gangestad, 2006; Pillsworth & Haselton, 2006). For example, a woman mated to a man of high genetic quality would have gained little genetic benefit from an extra-pair affair; the "good genes" she could have potentially obtained for her offspring would have been, at best, minimally superior to those she could have obtained by copulating with her long-term mate. Such minimal benefits are unlikely to offset the potential costs of such an affair. On the other hand, a woman mated to a man of low genetic quality could have reaped substantial genetic benefits by engaging in short-term liaisons with a man of high genetic quality (Gangestad et al., 2005; Haselton & Gangestad, 2006; Pillsworth & Haselton, 2006).

Women's short-term mating psychology may also serve additional functions besides the acquisition of high quality genes for their offspring. These additional functions include long-term mate-switching (Greiling & Buss, 2000), obtaining valuable resources (Symons, 1979), securing physical protection (Smith, 1984; see also Smuts, 1985), and elevating their social status by consorting with high-status men (Smith, 1984). Among men, androgenization is associated with the ability to effectively provide protection (Archer & Thanzami, 2009; Brewer & Riley, 2009) as well as social status and resource earnings (Newman, Guinn Sellers, & Josephs, 2005). Consequently, ancestral women would have been more likely to secure these benefits when they selected androgenized men as their short-term mating consorts. Regardless of which specific functions were served by women's extra-pair affairs (good genes, economic resources, physical protection, or more than one of these), the benefits of such an affair would have been greater, on average, for women mated to less androgenized men than for those mated to highly androgenized men (see Greiling & Buss, 2000).

This reasoning points toward the overarching hypothesis of a link between the alleles that ancestral men possessed at androgenization-linked genetic loci and their likelihood of facing sexual infidelity by their long-term mates.

4. The androgen receptor (AR) gene

The AR gene is an androgen-activated transcription factor that regulates gene expression throughout the brain and body (Bhasin, Woodhouse, & Storer, 2001; Simerly, Chang, Muramatsu, & Swanson, 1990). In humans, the AR gene is polymorphic, with the number of CAG codon repeats in the first exon ranging from nine to 31 (Alevizaki et al., 2003; Edwards, Hammond, Jin, Caskey, & Chakraborty, 1992; Lukaszewski & Roney, 2011; Simmons & Roney, 2011). Shorter sequences of CAG repeats are associated with greater expression of the AR protein (Choong, Kemppainen, Zhou, & Wilson, 1996) and enhanced transcriptional activity (Chamberlain, Driver, & Miesfeld, 1994). Consequently, shorter sequences of CAG repeats translate into stronger phenotypic effects of androgens. For example, men with fewer CAG repeats exhibit a greater physiological response to testosterone than do men with a longer sequence of CAG repeats (Zitzmann & Nieschlag,