



## Variation in CAG repeat length of the androgen receptor gene predicts variables associated with intrasexual competitiveness in human males

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### ARTICLE INFO

#### Article history:

Received 16 March 2011

Revised 9 June 2011

Accepted 15 June 2011

Available online 22 June 2011

#### Keywords:

Androgen receptor gene

CAG

Testosterone

Strength

Dominance

Prestige

Human mating

### ABSTRACT

An expanding body of research suggests that circulating androgens regulate the allocation of energy between mating and survival effort in human males, with higher androgen levels promoting greater investment in mating effort. Because variations in the number of CAG codon repeats in the human androgen receptor (AR) gene appear to modulate the phenotypic effects of androgens – with shorter repeat lengths associated with greater androgenic effects per unit androgen – polymorphisms in this gene may predict trait-like individual differences in the degree to which men are calibrated toward greater mating effort. Consistent with this, men in the present study with shorter CAG repeat lengths exhibited greater upper body strength and scored higher on self-report measures of dominance and prestige, all of which are argued to be indices of mating effort. Repeat length failed to predict sociosexual orientation (i.e. pursuit of short-term mating relationships), however, suggesting that the traits correlated with this polymorphism may be primarily associated with intrasexual competitiveness in the service of long-term mating effort. None of these measures of mating effort was related to baseline testosterone concentrations (either as main effects or as interactions with CAG repeat length), implying that long-term androgen exposure associated with AR gene polymorphisms may account for more variance in some androgen-dependent traits than does current testosterone concentration. These findings provide further evidence for the importance of the CAG repeat polymorphism in the AR gene in explaining a broad range of individual differences in human males.

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### Introduction

Polymorphisms in the human androgen receptor (AR) gene may play an important role in the explanation of individual differences in human morphology, cognition, and behavior. The number of CAG codon repeats in the first exon of this gene typically ranges from 9 to 31 in non-pathological populations, and tends to be normally distributed (e.g., Alevizaki et al., 2003; Edwards et al., 1992). Smaller numbers of CAG repeats are associated with both greater AR protein expression (Choong et al., 1996) and enhanced transcriptional activity of the AR (Chamberlain et al., 1994), suggesting that the same doses of androgen should be translated into larger phenotypic effects in men with fewer repeats. Consistent with this, physiological responses to testosterone treatment were negatively associated with CAG repeat length in a sample of hypogonadal men (Zitzmann and Nieschlag, 2007). This stronger mapping of androgen into phenotypic effects may in turn explain why shorter repeat lengths have been associated with androgen-dependent outcomes such as increased risk of prostate

cancer (Casella et al., 2001) and enhanced spermatogenesis (von Eckardstein et al., 2001).

Because the AR is a ligand-activated transcription factor – i.e. it regulates the expression of various genes when bound to androgens – the AR gene could act as a dial that calibrates the expression of diverse phenotypic traits in response to androgens. AR is expressed throughout the brain and body (Bhasin et al., 2001; Simerly et al., 1990), where it regulates different genes in different cell types, such that changing the number of CAG repeats in the AR gene alone could potentially dial up or down the degree of androgenicity across the entire organism. Such whole organism effects in principle allow coordination of morphological traits, such as body size and strength, with brain mechanisms that regulate behavioral patterns in which these features are instrumental, like degree of competitiveness, status-seeking, and interpersonal dominance. As such, AR polymorphisms may explain variability within a functionally coordinated suite of traits. Identification of the specific traits in question can in turn be derived from theories of the functional roles of androgens.

A number of theorists have advanced the idea that androgens are designed to adaptively regulate energy allocation between mating effort (not just the act of pursuing or competing for mates directly, but also securing status/resources to facilitate mate acquisition) and survival effort (Bribiescas, 2001; Ellison, 2001; McIntyre et al., 2006;

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Muehlenbein and Bribiescas, 2005). In humans, androgens promote anabolic processes (e.g., the accretion and maintenance of muscle mass; Bhasin et al., 2001) and have been linked to status-seeking and dominance-related behaviors (see Archer, 2006; Josephs et al., 2006; Mazur and Booth, 1998), all of which likely facilitate intrasexual competition. Conversely, androgens appear to inhibit survival-related outcomes, such as the capacity to mobilize immune responses and sequester energy reserves in adipose tissue (for review, see Muehlenbein and Bribiescas, 2005). Furthermore, these tradeoffs can be dynamically regulated through the adjustment of circulating androgens: men's testosterone is elevated when mating effort can produce greater benefits (e.g., when single vs. partnered, Gray et al., 2002, 2004; when in the presence of potential mates, Roney et al., 2007, 2010), but declines under conditions of food shortage (Bribiescas, 2001; Trumble et al., 2010) and immune challenge (Muehlenbein et al., 2005; Muehlenbein et al., 2010; Simmons and Roney, 2009).

Given that CAG repeat number in the AR gene appears to modulate the phenotypic effects of androgens, the same distinction between mating vs. survival effort critical in crafting a functional analysis of the effects of testosterone should likewise predict the specific traits associated with polymorphisms in the AR gene. Essentially, we propose that superimposed on the state-like changes in androgens associated with life-history problems will be trait-like individual differences in the degree to which androgens are mapped into increased mating and decreased survival effort. The current research focused specifically on mating effort, and tested the broad hypothesis that men with shorter CAG repeats will on average score higher on morphological and psychological measures of such effort than will men with larger numbers of repeats.

While no studies examining the role of AR polymorphisms have been explicitly framed in terms of the tradeoff between mating and survival effort, the extant evidence is broadly consistent with the idea that shorter CAG repeats (compared to longer) predict outcomes associated with greater investment in mating effort. For men in their twenties, CAG repeat number is negatively correlated with muscle size and lean body mass (Nielsen et al., 2010) and positively correlated with measures of body fat (Nielsen et al., 2010; Zitzmann et al., 2003), though evidence suggests that these relationships may not hold among older men (Walsh et al., 2005) or men in nutritionally stressed populations (Campbell et al., 2007). Although studies testing associations between AR gene CAG repeats and personality traits have produced mixed findings (see Jonsson et al., 2001; Loehlin et al., 2005; Turakulov et al., 2004; Westberg et al., 2009), when significant effects have been found, they have been in the direction of smaller numbers of repeats predicting higher dominance-related traits, such as extraversion, assertiveness, and verbal aggression (e.g., Jonsson et al., 2001; Lukaszewski and Roney, 2011). Men with shorter CAG repeats may be more common among criminal populations (Cheng et al., 2006; Rajender et al., 2008), especially violent criminals (Rajender et al., 2008), suggesting that such men may be calibrated to engage in particularly intense intrasexual competition. Finally, physiological correlates of shorter CAG repeat lengths in men include both higher rates of sperm production (von Eckardstein et al., 2001) and larger testosterone responses to social interactions with women (Roney et al., 2010). The latter finding in particular links AR gene polymorphisms to human mating psychology, and in conjunction with the morphological correlates of CAG repeats, supports the possibility of coordinated adjustment of diverse traits associated with mating effort.

The present study provides a focused test of whether AR gene polymorphisms have coordinated effects on both physical and behavioral/psychological variables. As intrasexual competition has likely played a critical role in the dynamics of human mating (both in direct competition for women and facilitating their mate choice), men's upper body strength was examined as a measure of physical

investment in mating effort. Shorter CAG repeats have been found to predict greater muscle mass in young men (Nielsen et al., 2010), but direct measures of physical strength have not been reported. Although muscle mass likely predicts physical strength, androgen-dependent variables such as rate of glucose uptake in muscle tissue (see Tsai and Sapolsky, 1996) or levels of hemoglobin (Zitzmann and Nieschlag, 2007) may alter strength per unit muscle mass. As such, actual strength (as opposed to muscle mass alone) may provide a more complete measure of physical investment in mating effort. It has been argued that upper body strength is the single most important predictor of success in men's physical conflicts (Sell et al., 2009). Winners of such contests enjoy both greater status and reproductive success among hunter-horticulturalists (von Rueden et al., 2011), supporting the idea that strength is directly relevant for mate competition under the approximate social conditions thought to characterize most of human evolution.

The degree to which men pursue social status was examined as a behavioral/psychological indicator of mating effort, as social status (and the associated command of resources) is argued to be an important factor in female mate choice (Buss, 1989). Evidence from hunter-horticultural societies supports a positive relationship between peer-nominated status and measures of mating success (Chagnon, 1988; Darwin, 1871; Irons, 1979). As status is an intrinsically scarce resource, however, men who pursued it have likely incurred significant risks due to intrasexual competition, and thus one expects on functional grounds the existence of mechanisms that calibrate status-seeking to cues of its current risk-reward ratio. Androgens appear to play a signaling role in such mechanisms insofar as they have been positively associated with decisions to compete with other individuals (Carre and McCormick, 2008; Mehta and Josephs, 2006); as such, shorter CAG repeats in the AR gene should (all else equal) similarly bias men toward greater willingness to compete for status. Measurement of status-seeking is somewhat complicated by the idea that status can be achieved through two theoretically distinct pathways: dominance, in which the application (or threat) of force is used to influence the division of resources by others, and prestige, in which resources are freely allocated to individuals based on their ability to confer benefits (Henrich and Gil-White, 2001; Johnson et al., 2007). A self-report measure with both dominance and prestige subscales (see *Methods*) was therefore used to measure status-seeking.

Finally, the present study assessed relationships between AR polymorphisms and self-reported measures of mating strategy. Various lines of evidence suggest that humans have had at least mildly polygynous mating systems throughout most of their history (e.g., Marlowe, 2003), in which case the pursuit of multiple partners may have been a mechanism whereby men's social status could be translated into greater reproductive success. If so, investment in physical strength, the pursuit of social status, and the desire for and pursuit of multiple sexual partners may all have been coordinated components of greater investment in mating effort. The sociosexual orientation inventory (SOI) is a validated measure of willingness to engage in sex without closeness or commitment (Simpson and Gangestad, 1991), and its items in part tap desire for sex with multiple partners. Some evidence supports positive associations between men's testosterone and their SOI scores (at least for men in relationships; see McIntyre et al., 2006), suggesting that shorter CAG repeats in the AR gene should likewise predict higher scores on this scale.

In summary, smaller numbers of CAG repeats in the AR gene were hypothesized to predict greater upper body strength, higher self-reported dominance and prestige, and higher SOI scores. Because these dependent variables could have causal relationships with each other (for instance, if greater physical strength caused greater dominance or higher prestige), exploratory analyses also tested whether individual outcome variables mediated relationships between repeat length and the other dependent measures.

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