Penultimate draft — Please cite published version.

Cognitive Traits as Sexually-Selected Fitness Indicators

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Abstract

The evolutionary psychologist Geoffrey Miller has argued that various features of human psychology have been sculpted, at least in part, by the evolutionary process of sexual selection via mate choice. This paper specifically examines the central claim of Miller's account, namely that certain cognitive traits have evolved to function as good genes fitness indicators. First, I expound on and clarify key foundational concepts comprising the focal hypothesis, especially condition-dependence, mutation target size, and mutation-selection balance. Second, I proceed to highlight some subtle distinctions with respect to the concepts of exaptation and adaptation, as well as Fisherian runaway selection and good genes sexual selection, all of which in turn bear importantly on the overall framework of cognitive traits as fitness indicators. Third and finally, I close out the paper by examining various conceptual and methodological criteria which are integral to identifying sexually-selected adaptations, then briefly examine some empirical work that has aimed to test the hypotheses that traits such as humor and creativity function as sexually attractive fitness indicators.

Keywords: evolutionary psychology, sexual selection, mating, good genes, mutation, cognition, fitness, Darwinism, evolution, runaway selection, creativity, humor

Introduction

The evolutionary psychologist Geoffrey Miller (2001) has argued that human cognitive evolution has been sculpted in part by sexual selection. Specifically, he believes that many human cognitive and behavioral universals such as music, humor, storytelling, and moral virtues are at least to some extent a result of an evolutionary history impacted by sexual selection via mutual mate choice (Miller, 1999, 2000a). Miller's theory ultimately is anchored in costly signaling theory, otherwise known as the "handicap principle" (Zahavi, 1975), and the central idea set forth is that various human capacities such as art, music, humor, moral virtue, and creativity have evolved as fitness indicators (in the evolutionary-biological sense) by dint of the fact that they are costly signals. Such cognitive and behavioral manifestations are taken to be costly due to their energetic costs; maintenance costs; time investment in order to develop and hone; conspicuous precision; and wastefulness, amongst other things. According to this reasoning only those individuals capable of taking on the opportunity costs of developing such traits will in fact be able to do so. More colloquially, those organisms without the requisite resources for investment will be forced to wear their disadvantaged state on their proverbial sleeve. Moreover, one of the upshots of the theory is that it was sexual selection via mate choice that was at least partly responsible for the (approximate) tripling in brain size during human evolution (Miller, 2007). More generally, sexual selection, a process first detailed by Darwin (1871), has experienced a renaissance in recent decades within ethology (e.g., Andersson, 1994), so its applicability is certainly not without precedent.

According to Miller, the human tendency to display creativity, to take just one of his examples, evolved at least partly because of its excellent role as an authentic signal of underlying genetic and phenotypic quality. Correspondingly, so the theory goes, the matching preference for

creativity in potential mates evolved because it served as an effective means to ascertain the phenotypic condition and genetic quality of those potential mates displaying the focal trait in question. It is the costliness of the creative products engendered by the capacity that vouchsafe them the status of being an authentic signal of genetic quality. Therefore, it is for that reason that it redounds to the benefit of perceivers to have evolved to be attentive to, and discerning of, such signals. Miller contends that, insofar as the mating domain is concerned, we have evolved adaptations that ultimately are tasked with appraising the mutation load of prospective mates through the signals they broadcast. To take the example of creativity, high-quality creative displays, such as witty use of language or artistic productions, are effectively honest advertisements that signal to the co-evolved, matching adaptations in receivers that the authors of those signals are relatively free of harmful mutations. Hence, such individuals possess good genes that can be passed on to progeny. The preference, therefore, acts as an indirect means of assaying the mutation load of potential mates—its ultimate evolutionary rationale—and its function is mediated by the proximate cognitive processes that recognize and admire the virtuosity conveyed via the signal.[1]

This paper will expound on and clarify the key foundational concepts of the theory advanced by Miller (2001). It will then be argued that (1) the g-factor of general intelligence comprises a substantial subset of an f-factor of overall fitness, (2) that the g-factor is hence an excellent candidate for serving as a window onto the overall mutation load of an individual, and (3) that general intelligence might accordingly mediate the expression of sexually-selected traits such as humor and creativity, the latter of which might hypothetically serve as an honest signal

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[1] I use the term "cognitive processes" in a broad sense so as to also encompass raw phenomenological phenomena such as emotions and other affective states associated with such appraisals.

of an individual's underlying genetic and phenotypic quality. The second half of the paper will then provide an analysis of conceptual subtleties relevant to the relation between exaptation and adaptation on the one hand, and Fisherian runaway selection and good genes sexual selection on the other, and in doing so argue that such subtleties are integral to understanding the processes by which traits might hypothetically evolve to function as fitness indicators. Specifically, it will be argued that traits which evolved for other purposes may potentially become exapted and then adaptively altered or extended by sexual selection for new or additional functions specifically as fitness indicators. And it will be argued that Fisherian runaway selection or sensory/cognitive biases can drive the evolution of traits to an extent that transforms them into highly condition-dependent traits, and hence legitimate candidates for use as good genes fitness indicators. Finally, various conceptual and methodological criteria of relevance to investigating and identifying sexually-selected adaptations will be outlined, followed by examining creativity and humor as traits that might hypothetically have evolved via sexual selection to function as fitness indicators.

Heritable variation in fitness

The theory that human's choose mates at least in part on cognitive traits which serve as reliable indicators of underlying genotypic and phenotypic quality presupposes, of course, individual variation in fitness. Interestingly, this presupposition parallels a question that has been posed in the non-human animal literature with respect to mate selection for putative good gene traits as well. The question just alluded to—often dubbed the "lek paradox"—asks what benefit might still be accorded to, say, the females in lekking species who still expend time to assess males who conglomerate in lekking areas and engage in mate display. Lekking species are those

that have been impacted by sexual selection in such a way such that one sex convenes at a single area at some specific time for the purpose of displaying particular traits to the opposite sex, in the hopes that those members of the opposite sex will choose those displayers as mating partners (Tomkins, Radwan, Kotiaho, & Trengenza, 2004). Supposedly, the paradox arises given the assumption that if females have been selecting for the fittest males as mating partners for a sufficient amount of evolutionary time, there should no longer be any meaningful genetic variance in fitness between males. That is to say, all of the fittest genetic variants should have already swept to fixation in the gene pool, such that all organisms within the population would be expected to possess those fittest variants. Therefore, since it apparently stands to reason that there is no such genetic variation in fitness among males, both sexes are expending costs without reaping any fitness benefits. Despite this expectation, however, male mating success is found to be positively correlated with time spent by males at lekking areas, both in absolute terms and relative to other males; frequency of intra-sexual fights with other male conspecifics; overall size of extravagant traits; as well as age (Fiske, Rintamäki, & Karvonen, 1998). Although one might suppose that the persistence of lekking might owe to some evolutionary constraint that forecloses its elimination in the species—to name just one possible hypothetical reason—the so-called paradox can be approached in another manner—one that takes the possibility that genetic variance in fitness may continuously persist.

For some time the canonical view held that traits most closely related to fitness would not remain heritable for very long—that is, would not exhibit inter-individual variation—since according to the work of R. A. Fisher (1958) the fittest alleles for such traits would eventually sweep to fixation in the population. Indeed, the lek paradox is seemingly diagnosed by way of this axiom of the standard Fisherian story. According to the Fisherian formulation, this is also to

be expected particularly in the case of lekking males, whose traits under scrutiny by female conspecifics would be under particularly strong selection—as it is those focal traits which determine which of the males reproduce. For instance, empirical analyses found life-history trait heritabilities to negatively correlate with the amount of reproductive success those traits explained. Since life-history traits were assumed to be central to fitness, and since those traits did not appear to be very heritable, the conventional interpretation seemed vindicated—as, once again, it was thought that low heritability was a sign of selection having caused the fittest variants to sweep to fixation in a population. To put the point differently, it was assumed that a lack of genetic variation between individuals in traits thought to be central to fitness was a sign that selection had driven the fittest variants to fixation in the population or species in question. More precisely, it was reasoned that low heritability was tantamount to low additive genetic variance.

However, this reigning assumption was eventually questioned by various researchers. It was found, on the contrary, that the traits most tied to fitness were rather those with the *most* genetic variation among individuals. What appeared to mislead many was the fact that complex life-history traits exhibited relatively large amounts of environmental variation, leading to low heritabilities, and hence obscured the degree to which those traits actually contained additive genetic variance (Price & Schluter, 1991). Life-history traits are those which in general are linked to an organism's reproductive fitness—i.e., juvenile survival, rate of development, longevity, age-specific fecundity (Hughes & Burleson, 2000). Any trait's heritability, including that of life-history traits, is the proportion of phenotypic variation in a given population explained by genetic variation (V_G). h^2 typically symbolizes a trait's "narrow-sense heritability", which is the extent to which its phenotypic variance can be accounted for by the additive (linear)

effects of genes—in other words, the precise sense in which, say, three specific alleles (gene variants) additively affect a specific trait. By contrast, a trait's "broad-sense heritability" (H^2) encompasses both its narrow-sense heritability plus, in addition, all of its phenotypic variation due to non-additive (non-linear) factors such as *dominance* and *epistasis* (Hughes & Burleson, 2000)—with dominance defined as the masking effect that one allele can potentially exert on another at the same genetic locus, and epistasis defined, roughly, as the effect(s) that two or more alleles at two or more loci can exert in virtue of their unique interactions with each other. Just as importantly, all of a trait's variation not accounted for by genetic variation is subsumed by its environmental variance (V_E). A key realization was made when it was discovered that life-history traits frequently evince low heritabilities, and hence a large degree of environmental variance, despite *significant* amounts of genetic variation (Houle, 1992).

Again, life-history traits were taken to lack additive genetic variance since researchers assumed (erroneously) that heritabilities were a good proxy measure for it. Houle (1992) also devised a standardized way of comparing traits for additive genetic variance, both within and across species, through measuring coefficients of additive genetic variance (CV_As). Narrow-sense heritability measures, on the other hand—what researchers had been utilizing to assess additive genetic variance—simply do not allow for such comparisons to be made. Indeed, although it is minimal, evidence suggests that when utilizing the mean-standardized measure of coefficient of additive genetic variation, human fitness components do in fact exhibit levels of variation on par with that seen in other experimental species in the literature (Hughes & Burleson, 2000). That there is such additive genetic variation in fitness components, in turn, is partly but importantly explained by the highly polygenic architecture of such traits (Merilä & Sheldon, 1999), to be discussed next.

Costly signaling, condition-dependence, mutation target size, and mutation-selection balance

Four of the key related concepts in the theory of human cognitive evolution via mutual mate choice are costly signaling, condition-dependence, mutation target size, and mutation-selection balance. To begin with, *condition-dependence* refers to the manner in which a given trait's expression is contingent on the overall condition of an organism. To take the well-worn textbook example of the peacock's tail, the standard reasoning is that only those peacocks in the best overall condition—i.e., strong immunocompetence, parasite- and pathogen-free—can effectively grow the tails that peahens find the most attractive—viz., large tails with radially-symmetric eye spots and vibrant colors. A trait's potential role as a window on the underlying genetic quality of an organism thus becomes enhanced to the extent that its development captures ever-greater amounts of the genome—that is, to the extent that a larger proportion of the genome is implicated in its development and expression, either directly through its mutation target size, or its condition-dependence more generally. Only those individuals best able to afford the allocation of resources (i.e., time and energy) and buffer against pathogens, developmental anomalies, and so forth, are able to develop such costly indicator traits. Hence, such traits are precisely those that are the most condition-dependent.

Condition, then, is a reflection of genotypic quality. Another way of illustrating the nature of a condition-dependent trait would be to imagine a species whose brightly colored plumage evolved as a sexually-selected indicator trait. In this hypothetical example, it may be that the bright plumage evolved as such because those organisms who could display it at brighter than average levels were generally in better overall condition, and hence could pay the costs of

being more conspicuous to predators within their niche. In other words, such brightly colored peacocks can afford to make themselves more visible to predators, vis-à-vis their not-so-brightly colored conspecifics, presumably because they possess characteristics that make them more efficient in identifying, evading, or escaping from predators, by dint of their genotypically-mediated superior condition. Condition in this sense, therefore, would be thought to be substantially reflective of underlying genetic quality, substantial enough to have exerted a selection pressure on mate choosers to be attentive to it.

Rowe and Houle (1996) argued that an indicator trait that has been forged by sexual selection can come to depend on the functional efficiencies of very many other traits in the organism. For instance, if a given animal must allocate a high proportion of its food intake into the growth of an indicator trait, it must, among other things, be highly effective at hunting, scavenging, or foraging for food, which in turn hinges on the effectiveness of many of its other traits—i.e., visual acuity, stealth, speed, tracking, etc. Individually, each trait taken in isolation is a window on perhaps a small portion of the functional genome. But in aggregate, the composite of traits represents a much wider window. And since a sexually-selected indicator trait's quality comes to depend so crucially on the efficiency of all of these traits, the indicator trait itself effectively becomes a reliable window onto the portion of the functional genome which impinges on the ontogeny and expression of each of those constituent traits. As one concrete example of condition-dependent indicator traits, consider the work of Cotton, Small, Hashim, & Pomiankowski (2010), who found that the sexually-selected eyespan of male stalk-eyed flies—wherein males possessing longer eyespans are preferred as mates by females—covaried with other fitness-related traits, namely the size of their accessory glands and testes. Furthermore, these associations persisted even when controling for body-size, thus the researchers were able to

eliminate the possibility that a generalized body-wide allometric relationship explained the correlation. Cotton et al. (2010) also found that female stalk-eyes face the recurrent challenge of severe sperm-limitation in their natural ecology, and so benefit from larger supplies of sperm. To this end, females also preferred mating with males possessing the largest reproductive organs, as those males were capable of mating at high-frequencies and/or inseminating them with larger stores of sperm per ejaculate. Cotton et al. (2010) argue that the correlations between all of these focal traits are most plausibly explained by condition-dependence, with organisms in the best condition most able to develop and maintain such costly traits.

Miller's (2001) account gets particularly interesting precisely due to the fact that the cognitive and behavioral traits he thinks were shaped by sexual selection via mate choice are those which are likewise highly condition-dependent. To this end, he argues that since approximately half of the human genome is implicated in brain development, any human capacity that utilizes a significant proportion of the brain for its genesis—that is, for its cognitive and behavioral development and display—may serve as an especially effective means for advertising the user's underlying phenotypic and genotypic quality. Moreover, the proportion of the genome implicated in the ontogeny and expression of a given trait is taken to be its *mutational target size*. Accordingly, a trait's mutational target is the protein-coding and regulatory regions of the genome implicated in the focal trait's development, expression, and maintenance, and at which non-neutral mutations can occur and accumulate, thus directly degrading or disrupting the quality of that very trait.

A central mechanism expected to generate much if not most of the genetic variance in fitness across species in general, but specifically in our case within humans, is mutation. And the process of *mutation-selection balance* is one central mechanism that can give rise to such

heritable variation in fitness. As applied to the theory of sexual selection, the focal traits postulated to function as good genes indicators are taken to be highly polygenic—hence their large mutational target size—and so there are many more genetic loci at which mutations can exert a negative effect. On the whole, most mutations that are not lethal produce relatively minor decrements in overall fitness on average. Hence, such mutations can persist in populations for many generations before being eliminated. Broadly speaking, the contribution of mutation-selection balance to variance in fitness within a population is a function of U, the rate of deleterious mutation per diploid genome per generation, which in turn is a function of the average rate of mutation per locus combined with the total number of functional loci within the genome. Researchers have estimated U to be between 1.8 to 2.0 (Eyre-Walker, Woolfit, & Phelps, 2006; Nachman & Crowell, 2000). As Thornhill and Gangestad (2008) put it, "If U is 2 and the mean effect of mutations on fitness has been 1–3% in humans, the population degrades in fitness by 2–6% per generation by fresh deleterious mutation alone" (p. 149).[2]

Almost all mutations are many generations old, having accumulated over time and persisting due to their relatively minor (yet still harmful) effects on fitness. As per mutation-selection balance, these minor yet harmful mutations can individually persist for many generations before finally being purged by selection. Due to the highly polygenic nature of postulated indicator traits, it is therefore easier for such mutations to accumulate within an individual's lineage and be phenotypically expressed as a function of that individual's mutation load. Evolutionary-genetic predictions hold that the majority of older, accumulated mutations

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[2] If these estimates of mutation rate and their effects on functional, fitness-impacting traits are conservative and the real figures turn out to be greater, it would suggest that mutation might be even more of an evolutionary concern so far as fitness goes—at least theoretically speaking.

will lessen fitness anywhere between approximately 0.00005% and 0.05%. To put this range in perspective, consider that a mutation that reduces the number of surviving offspring by 1% will persist in a large gene pool for an average of approximately 10 generations, passing through approximately 100 individuals in the process (Penke, Denissen, & Miller, 2007). Furthermore, a mutation with even a *0.1%* reduction in fitness—notably still 10 times stronger than what selective neutrality would be in humans—will still persist for 14 generations (Garcia-Dorado, Caballero, & Crow, 2003).

Estimates of the number of old, minor mutations expressed by chromosomal loci affecting the brain in some manner via protein-coding effects range from 500 to 2 000 (Keller & Miller, 2006). This count should perhaps be doubled to account for mutations that disrupt brain-relevant regulatory regions, and, in addition, mutational effects stemming from indels and translocations (Keller & Miller, 2006). Given these figures, on the order of 500 mutations of all effect types would disrupt the brain on average. But since humans also likely exhibit high between-individual variance in both the number of mutations possessed (mutation load) and the effect magnitude that any one mutation exerts, not every individual would therefore be equally affected by mutation (Keller & Miller, 2006). Such variance would additionally also be expected to be compounded given assortative mating for genetic quality in humans. The concept of assortative mating refers to the tendency of individuals to mate with those who possess traits similar to their own, for instance age, religiosity, political orientation, education, intelligence, and height (e.g., Watson et al., 2004).

A brief recapitulation of some of the concepts explored hitherto will help to take stock of the theory so far. As highlighted in the foregoing, mutation-selection balance is a key component in Miller's account of human mental evolution. It is because of this that the postulated

underlying rationale behind the evolutionary impetus of sexually-selected, condition-dependent indicator traits is the inability in many cases of selection to purge organisms of harmful mutations at a rate proportional to their genesis (Keller, 2008). Said differently, the rate of mutation in these cases outstrips the rate of purifying selection within various species. Moreover, and importantly, some organisms within those species carry more harmful mutations than other conspecifics.[3] Such a set of contingent facts can therefore place selection pressures on organisms to evolve mate preferences for indirectly assessing a potential mate's mutation load. Correspondingly, it pays the most fit, mutation-free organisms to evolve costly, condition-dependent signals that advertise that fact. Interestingly, some empirical evidence suggests that good genes sexual selection via mate choice is in fact effective at purging harmful mutations (Hollis, Fierst, & Houle, 2009), as well as increasing mean species fitness and facilitating adaptation to an environment (Lorch, Proulx, Rowe, & Day, 2003; Fricke & Arnqvist, 2007). Indeed, Agrawal (2001) and Siller (2001) argue that the very reason that sex itself has been maintained is for the *purpose* of reducing mutation loads.

The *g*-factor of general intelligence and the *f*-factor of fitness

Another central feature of Miller's overall theory is the function of general intelligence within the context of mating. Miller (2000b) holds that the *g*-factor of general intelligence (Jensen, 1998) parallels what might be called the *f*-factor of fitness. On the one hand, psychometric *g* taps a wide network of cognitive abilities—e.g., processing speed, visual perception, memory, retrieval ability—each of which is positively inter-correlated with all of the

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[3] For a laboratory study that also found an instance of condition-dependent mutation rates—that is, differences in the mutation *rate* between individuals, owing to their condition—see Agrawal and Wang (2008).

other factors. The *g*-factor therefore sits as a latent, superordinate factor at the top of a hierarchy composed of positively correlated sub-factors—with the aggregate of these all-positively inter-correlated sub-factors otherwise known as the "positive manifold". On the other hand, fitness might similarly be measured using an overall *f*-factor: Like the *g*-factor, each constituent trait of an organism which is implicated in its fitness constitutes a subordinate component, and all such traits collectively as an aggregate are measured by the superordinate fitness factor *f*. As with the all-positive inter-correlations among the constituent cognitive factors inhering in the hierarchical manifold of *g*, fitness components, too, exhibit positive correlations with each other. As already mentioned earlier, since much of the functional genome is expressed in the brain and implicated in its development, and because the *g*-factor, in turn, is a superordinate factor tapping a very expansive array of sub-factors governing cognitive functioning, *g* therefore is potentially a *substantial subset* of an overall fitness factor (*f*). It stands to reason, therefore, that products of cognitive functioning may theoretically be revealing of much of fitness. That is, products of cognitive functioning may act as reliable indicators of underlying genotypic and phenotypic quality in proportion to the extent that they tap the *g*-factor. As such, highly creative and costly displays such as music, art, humor, and verbal wit may potentially be ideal vehicles which reliably transmit accurate and honest information about their producers' underlying fitness. This of course is not to say that such costly displays have in fact actually evolved via sexual selection to function as such. Rather, the important point here is to first establish a theoretical framework from which various empirical tests can be derived and possible design features investigated.

As already highlighted, it is empirically the case that the traits most directly tied to fitness in various animal species are those exhibiting the most heritable variance between organisms (see Thornhill & Gangestad, 2008, pp. 145–148). And because general intelligence in humans

also exhibits well established, highly heritable genetic variance between individuals (e.g., Plomin & Spinath, 2004; Posthuma, de Geus, Eco, & Deary, 2009; Segal & Johnson, 2009)—with molecular-genetic studies also confirming its heritable basis (e.g., Davies et al., 2011; Plomin et al., 2013)—it would certainly accord with Miller's overall thesis insofar as it, too, is a latent variable which correlates with the quality of hypothesized sexually-selected traits (e.g., creativity).

The *watershed model* (Cannon & Keller, 2005) helps to illustrate the pathways connecting mutations in functional regions of the genome to phenotypic traits. According to the model, harmful mutations at various genetic loci have disruptive effects on more basic "upstream" traits such as dopamine transmission in prefrontal cortex, with the disruptive effect of any one mutation depending on its severity. Such effects, in turn, can exert themselves on more "downstream" traits such as working memory, which feed into still more downstream traits such as overall cognitive ability. Moreover, mutations occurring at multiple loci can combine their effects at downstream sites where their disruptive contributions meet, and the combined effects of some mutations may perhaps owe their products to epistatic interactions (as per epistasis). Hence, mutations at multiple chromosomal loci can yield a cascade of disruptions that become ever larger as they run from upstream traits to progressively more downstream traits, the latter of which draw on a widening reservoir of disrupted upstream traits. As such, the watershed model is one way to conceptualize the biological pathways undergirding high-variance, condition-dependent, highly polygenic fitness traits, and it illustrates how such traits can be subject to mutational load, as per mutation-selection balance.

Developmental instability also provides an additional way of conceptualizing and illustrating how phenotypic traits are susceptible to various negative perturbations (Møller &

Swaddle, 1997). Developmental stability refers to the degree to which an organism can buffer its overall development against harmful perturbations induced by either genetic mutations, on the one hand, or disruptive influences such as toxins, pathogens, and stochastic events during ontogeny, on the other. Either type of developmental perturbation, singly or collectively, is taken to disrupt the functional fit between organism and environment. Empirical measures of the degree of symmetry in bi-laterally symmetrical traits, such as ear-length and ankle-breadth, are theoretically posited to be proxies for developmental stability, particularly when such traits are measured in aggregate (Gangestad & Simpson, 2000; Leung, Forbes, & Houle, 2000; Gangestad, Bennett, & Thornhill, 2001). Therefore, an organism's overall degree of bilateral symmetry is believed to represent the extent to which it is capable of developing stably, with higher overall symmetry indicative of greater developmental stability.

As an example of the postulated general fitness factor's potential applicability to concrete cases, consider sperm competition in male guppies, which has been demonstrated to yield offspring of higher quality (Evans & Magurran, 2000). As it turns out, some male guppies possess a capacity for higher rates of sperm production relative to other slower sperm-producing conspecifics, thus enabling them to crucially inseminate female mates with a larger relative sperm store. Furthermore, sperm production rate in guppies is correlated positively with both courtship intensity and body size, which are in turn cues used by females in mate choice (Evans & Magurran, 2000). Courtship intensity, body size, and sperm production all turn out to be condition-dependent traits, effectively allowing guppies with the best genes to reproductively outcompete conspecific males through sperm competition and by being selectively preferred by females.

Interestingly, recent evidence indicates that various indices of sperm quality are correlated with both body symmetry and general intelligence in humans (Arden, Gottfredson, Miller, & Pierce, 2009; Pierce, Miller, Arden, & Gottfredson, 2009). Pierce et al. (2009) argue that the link between sperm, body symmetry, and intelligence is mediated by the common underlying physiological pathways subserving such traits, which are likely explicable via the pleiotropic effects of genes—pleiotropic effects (or pleiotropy) referring to the phenomenon whereby a single gene affects two or more traits.

Pierce et al. (2009) additionally argue that cross-taxa similarities in the link between good genes and quality sperm may be explained by the highly conserved nature of such underlying biological pathways. Insofar as this take on matters is accurate, it is consistent with the view that cognitive traits might function as reliable, condition-dependent fitness indicators displayed in mating contexts. As we have seen, according to the view of cognitive traits as fitness indicators, indicator traits (e.g., creativity and humor) are taken to be correlated with general intelligence, which in turn is correlated with fitness (which, like general intelligence's theoretical relationship to the g-factor, can also be treated as a latent, superordinate factor—a "general fitness factor" (f)).

Exaptation to adaptation

Before discussing the conceptual relation of exaptation to adaptation, a related and relevant issue regarding the manner in which adaptations can come to be co-opted in the service of non-adaptive ends (Buss, Haselton, Shackelford, Bleske, & Wakefield, 1998) is worth highlighting. Pinker (1997), for instance, has argued that various human capacities such as music and humor were not directly selected for by evolution, but rather are capacities which we are

capable of by dint of intentionally co-opting various other selected-for adaptations, either singly or conjunctively, and utilizing them for such non-adaptive functions—where non-adaptive functions are here meant in the more stricter evolutionary-biological sense of non-adaptive, namely not conducing to genetic fitness. For instance, although humans possess a capacity to play baseball, the capacity itself certainly did not arise as a result of natural selection. And yet humans can co-opt a variegated array of cognitive and anatomical adaptations which thereby allows them to play that particular sport, even though, crucially, each of those particular adaptations which are tributary to playing baseball were not specifically selected for that purpose. Likewise, it might be similarly alleged that certain human capacities such as humor, and creativity more generally, were not sexually-selected but rather arise from the intentional co-opting of an assortment of cognitive adaptations that evolved for other functions, but which nonetheless can be flexibly deployed in the service of such evolutionarily-novel and non-adaptive roles. Ascertaining whether some trait is an intentional co-opting of one or more non-sexually-selected adaptation(s), or whether it was forged at least in part by sexual selection, will of course require careful research.

When assessing cognitive traits as hypothetical fitness indicators that were forged by sexual selection, a nuanced approach to the concept of exaptation is also requisite. For, as will be seen, there is no reason to expect that sexual selection will not also exapt structures and processes that evolved for some other functions and utilize them in generating fitness indicators. Such an exaptation of pre-existing adaptations can function in the new sexually-selected role alongside the pre-existing role(s), or else become the exclusive function which selection is maintaining the trait for. Moreover, and as will be discussed, in exapting traits, sexual selection can alter and extend them in ways which enhance their new roles—that is, the roles they play in

generating fitness indicators. For example, it is hypothetically possible that our linguistic faculty was in part altered or built upon by sexual selection to function as tributary to some fitness indicator(s). If so, at a broad level of analysis, the functioning of our larger adaptation for language is very likely to submerge a more fine-grained and specifically sexually-selected purpose which might inhere within it.

Similarly, many other brain and cognitive systems that originally evolved for other purposes may have likewise been altered or extended by sexual selection. The upshot of such considerations, therefore, is that it would be hasty and misguided to conclude that any degree of exaptation is tantamount to a lack of sexual selection. And similarly, what might appear upon first glance as an intentional co-opting of various adaptations in the service of an apparently non-adaptive function might conceivably turn out to be a larger trait whose constituent components were linked together by sexual selection over evolutionary time for the purpose of functioning as a fitness indicator—and even if some or all of those constituent components at least partly originally evolved for other purposes and still fulfill those functions (alongside the new sexually-selected function).

I will now set forth some brief conceptual clarifications with respect to exaptation, since it bears rather crucially on the analysis to follow, and ultimately on the plausibility of Miller's (2001) theory of human mental evolution. To begin with, a critical distinction has been drawn by Andrews, Gangestad, and Matthews (2002) with respect to *primary exaptation* and *secondary adaptation*. Primary exaptation occurs when an adaptation, whose etiology traces to the effect(s) in virtue of which it was naturally-selected, becomes pressed into service for a new or additional function other than the one it was originally selected for. This new or added function, like the original one, also contributes to the fitness of an organism, owing to the new selection

pressure(s) which now obtains to maintain the trait in the population. Crucially, however, the difference between the exapted function and the original function is that the former does not owe its existence in the first place to being naturally-selected for the new effect(s) it now gives rise to, whereas the latter does. Secondary adaptation, on the other hand, occurs whenever an exaptation, in response to some new selection pressure(s), becomes altered or extended in some way. This nuanced distinction is rather important to bear in mind, given the amount of confusion that has been sown by the term exaptation.

Technically speaking, therefore, even the most subtle of alterations or extensions to an exaptation in response to some new selection pressure(s) qualifies the new function as adapted. But crucially, the transition that a primary exaptation may make to a secondary adaptation is a matter of degree. A secondary adaptation can be only minimally altered or extended, at one end of the continuum, or it may come to be heavily altered or extended, closer to the other end of the continuum. In principle, ontologically speaking, the selection pressure(s) which forged a given trait can be decomposed, such that selection pressures can be mapped on to its structures and processes—with each such structure or process being delineated in however fine-grained a way requisite to pick out all of the appropriate selection pressures which shaped it. Moreover, constituent structures and processes of a posited adaptation which were not directly selected for, but rather were forged as an ancillary effect of some other non-selectionist process, should similarly be possible to delineate, at least in principle. Whether in practice this will always be within our epistemic ambit to fully discover for any given trait is, of course, a different question. In any case, however, the line between primary exaptation and secondary adaptation can in principle be very slight, and in some cases ascertaining which is true will require much investigation and attention to the empirical details.

Perhaps more surprisingly, however, while Gould and Vrba (1982) helped make salient the phenomenon of exaptation, their paper has arguably shifted many scholars' attention away from just how blurry the line between a pure primary exaptation and secondary adaptation is. That is, in many cases one might be led to overlook the existence of adaptation, however slight, by not paying sufficiently close attention to the possibility that an exaptation has become better adjusted for its new function, and in so doing—and this is the crucial point—transform into a secondary adaptation.[4] Alternatively, exapted structures or processes can also come to feature as integral components of new adaptations, and that larger adaptation does not cease being an adaptation simply because it exapts one or more pre-existing components.

To illustrate the way in which an exaptation can become integrated with a new adaptation, consider first an example of primary exaptation. Although the black heron's wings evolved as an adaptation for flight, it nonetheless additionally utilizes those wings—that is, exapts them—for the purposes of preying on small fish. It is hence an example of primary exaptation, where a trait originally evolved for some prior function(s) is directly put into the service of a new one (and which may come to supplant entirely the previous function(s)). Even so, the black heron exapts its wings for the new function in conjunction with (presumably) some form of evolved neurocognitive circuitry in its brain that has additionally been designed specifically for utilizing those wings for the purposes of shielding the surface of the water, so as to get a clear view of the fish swimming underneath. As such, although its wings are thus properly construed as a primary exaptation, an equally interesting and important fact is that they

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[4] By speaking of the potential pervasiveness of adaptation here, I am not necessarily making the claim, sensu Godfrey-Smith (2001), that what he dubs "empirical adaptationism" is true (though it may be the case that it is). Nor am I necessarily making the claim, sensu Orzack and Sober (1994), that all adaptations are optimal (though it may be the case that they are).

are still part of an adaptation designed specifically for hunting small prey (namely fish). That is, in the case of primary exaptations, that such traits are exapted to a new function should not obscure the fact that they are still featuring in a larger adaptation that has evolved specifically for that function.

As Gould and Vrba insightfully brought to our attention, sometimes lack of appropriate concepts can obfuscate, if not obscure completely, important phenomena. But by the same token, sometimes concepts can become so reified that they effectively create artificial walls that nature does not even recognize. Ironically, Gould and Vrba's conceptual addition has oftentimes caused some thinkers to blur or miss completely this critical distinction, spuriously thinking that the presence of any exapted structure is tantamount to the absence of adapted structure, either within the exaptation itself or in the larger adaptation which it comes to functionally contribute to. Hence, many have missed the subtle line and dynamic interplay between the two phenomena of exaptation and adaptation. Just as importantly, it bears mentioning again that any primary exaptation that has undergone even the *slightest* of alterations or extensions by selection has technically become a *secondary adaptation* for the new task to which selection has ever-so-slightly honed it for. As an example, consider feathers. Although feathers per se first arose evolutionarily as an adaptation for thermoregulation, the ensuing changes that selection has exerted on them can be circumscribed as secondary adaptation. And since the difference between primary exaptation and secondary adaptation can be ever so slight, it should serve as a warning to be cognizant of the subtle, often ephemeral, line separating the two.

In a sense, therefore, the upshot of this closer analysis may be that the distinction between exaptation and adaptation may paradoxically be more than it has been made out to be.[5]

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[5] See Dennett (1995, Ch. 10) for much the same conclusion.

Perhaps it would be profitable to ask in each case the degree to which an exapted structure has possibly been altered by selection—that is, conceptualizing its change as running on a continuum rather than in discrete terms. As it turns out, the foregoing considerations are relevant to assessing the overall theoretical framework of cognitive abilities as fitness indicators, insofar as many of the constituent elements of such hypothetical fitness indicators originally evolved for purposes other than the ones they may have come to serve in mating contexts. Before moving on, however, it should be noted that some elements of hypothetical cognitive fitness indicators might still be serving more than just a purpose in mating, including more evolutionarily older purposes. For instance, Miller (1997a) provides an interesting discussion both of the possible phylogenetic provenance of protean cognition, and of the possible connections between protean cognition and creativity, particularly as the latter might function in courtship contexts. Processes of exaptation can also hypothetically occur by exapting adaptations that were possibly forged by gene-culture co-evolution and group selection. Investigating and testing sexual selection hypotheses might well require taking these considerations seriously as well.

Fisherian runaway and good genes models of sexual selection: diametric ends of the same continuum

In the animal behavior literature, *sensory and cognitive bias* has often been argued to be a theoretical explanation for the evolution of sexually-selected traits. Endler and Basolo (1998) outline a cluster of interrelated concepts regarding sensory and cognitive biases. For instance, males of a species may come to evolve sexual signals (i.e., brightly and distinctly colored plumage) if doing so taps into preexisting though latent sensory or cognitive biases which females of the species possess, and which also lead females to preferentially mate with the males

displaying such signals. This particular type of signal evolution is referred to as "sensory exploitation", since males effectively capitalize on and exploit the latent sensory or cognitive biases of female conspecifics if doing so makes themselves more attractive as mating partners. Such biases may exist for a variety of reasons, for instance as a result of sensory or cognitive adaptations that evolved for other purposes, but which nonetheless respond to stimuli that fall outside of the domain for which those adaptations were tuned by natural selection to attend to. To use a hypothetical example in the case of humans, creative cognition may have stimulated certain sensory or cognitive biases in ancestral humans in such a way that made them more attractive as mates. From here, the underlying capacity for creativity may have evolved further, as a result of the direct mating benefits that accrued to those who displayed such a trait. By contrast, it has been argued that sensory bias, rather than selection for good genes benefits, might explain at least some of the many instances of sexually-selected traits in various species.

Interestingly, it will turn out that in diagnosing the issues of sensory/cogntive bias and *Fisherian runaway selection*, either *can* collapse into good genes sexual selection over a sufficient stretch of evolutionary time. I argue that one error is to consider the Fisher runaway and *Zahavi good genes model* as mutually exclusive. The Zahavi good genes model refers to the process whereby some trait becomes selectively advantageous because it is preferred by mate choosers qua a costly good genes indicator—that is, as a highly polygenic, highly condition-dependent trait subject to mutation load. Fisherian runaway selection refers to the process whereby some trait evolves in response to a preference for it in the opposite sex, and typically quite rapidly by evolutionary standards. For instance, the peacock's tail is argued to have evolved via runaway: roughly, some preference in ancestral peahens caused them to prefer as mates mutant peacocks with tail feathers incipient to the ones found in contemporary peacocks,

though nonetheless elaborated enough to set those ancestral peacocks apart from males that did not possess them. The preferences of females for a flashier tail eventually lead those mutant peacock tails to eventually characterize all males of the species, as males with flashier tails left more offspring than conspecifics with less adorned tails. Depending on the nature of the female preference, it can set off an evolutionary cascade which causes peacock tails to continuously evolve into more elaborate and gaudy forms. Such a runaway effect can even continuously drive the evolution of some trait to become increasingly more ostentatious, up to the point where the costs (e.g., by making its possessors too conspicuous to predators) begin to outweigh the fitness benefits (via mating opportunities) (Pomiankowski & Iwasa, 1998). Fisherian runaway processes also tend to make both the trait and the preference for it more common in the gene pool, since offspring will tend to inherit the genes underlying both.

As we will see, researchers within the field have argued that the Zahavi good genes model, on the one hand, and the Fisherian runaway process and cognitive/sensory bias, on the other, are in fact really two extremes of the same continuum, and that both may figure in the evolutionary trajectory of a given trait. Here is where the preceding discussion regarding the tenuous line between exaptation and adaptation usefully sheds light on the situation. For it is perhaps easy to overlook the manner in which a trait might initially evolve via either pure Fisherian runaway selection or by tapping into the sensory bias of receivers only to at some point transition to a good genes indicator trait.

For a trait whose evolution has been powered by either sensory/cognitive bias or Fisherian runaway selection to transition to a good genes indicator, it need only be the case that the trait becomes sufficiently condition-dependent, such that it comes to function as an authentic advertisement of genetic quality. In other words, a trait that has evolved, say, via Fisherian

runaway selection (simply because there exists a preference for it in mate choosers) can potentially come to function as a good genes indicator if its development and expression becomes sufficiently dependent on an organism's overall condition, and hence an indicator of genetic quality (an index of mutation load). With such a state of affairs in place, the opportunity would arise, ceteris paribus, for the opposite sex (or conspecifics more generally, in the case of inter-sexual selection) to evolve appraisal mechanisms for the purposes of assessing genetic and phenotypic quality. Consider also Kirkpatrick's (1996) take on the matter in one specific context:

> ...simulation results suggest that the relative contribution made by the good genes process to the final product will not be large compared to that from direct selection. This scenario illustrates the fact that existence of a good genes process does not imply that it was the main force responsible for evolution of the male display. (p. 2134)

Kirkpatrick's statement here is interesting in relation to Miller's own hypothesis, mainly because Miller (2001) himself suggests that traits that end up as indicators of underlying genotypic and phenotypic quality can originally have been elaborated by standard Fisherian runaway selection. According to this view, at some point the elaborated trait sufficiently captures enough genetic information in the genome—that is, becomes highly condition-dependent—to effectively make it a good genes indicator. One might here imagine the evolution of the peacock tail initially evolving by means of sensory bias or Fisherian runaway, and in the process becoming a progressively more condition-dependent trait, whereupon it eventually evolves to become so condition-dependent that it effectively becomes a good genes indicator. In other words, a threshold is crossed, whereby the trait henceforth becomes directly selected as an indicator via

sexual selection for good genes. Another way of putting the point is to say that the evolutionary status of the trait experiences a phase transition, from Fisherian runaway to Zahavian handicap, upon which the trait is maintained or (typically) elaborated further, in virtue of its new status as a reliable indicator of genetic and phenotypic quality. In this sense, it is exactly a manifestation of the transition from *primary exaptation to secondary adaptation* that was outlined earlier, whereby a new selection pressure can "grab on" to the now highly condition-dependent trait in question, henceforth altering or extending it in the service of some new functional, adaptive purpose—in this case as a sexually-selected good genes advertisement utilized and appraised during courtship.

Of course, the specific threshold at which this might occur for any given trait or species is an empirical question. Also, as Endler and Basolo (1998) assert, the various processes of sexual selection can even function simultaneously:

Sensory-drive models are sometimes regarded as alternatives to adaptive mate choice [i.e., good genes selection] ... and Fisherian models ... but this is not realistic. Sensory drive can run simultaneously with both the FP [Fisherian runaway process] and GG [good genes selection] models. (p. 419)

The lesson here is that identifying sensory/cognitive bias or Fisherian runaway as a plausible explanation for the evolution of some trait must not come at the expense of hastily dismissing the possibility of good genes choice occurring as well. For animal species selecting mates via sensory/cognitive bias or Fisherian runaway selection may simultaneously be also selecting mates with good genes as well. Similarly, Payne and Pagel (2001) support Miller's construal of

sensory bias, as well as the related presentation I have given with respect to transitioning from runaway selection or sensory/cognitive bias to good genes selection: "Some commentators view sensory bias as sufficient by itself to explain contemporary signaling behavior, but others think of it mainly as a factor that might contribute to the initiation of alternative signaling processes" (Payne & Pagel, 2001, p. 42). Seminal and influential work by Grafen (1990) also highlights the nature of the underlying continuum, adjoined at opposite ends by Fisherian runaway and good genes selection, respectively:

> theoretically, the Fisher process is not a necessary part of models of sexual selection. Empirically, it is an open question whether the Fisher process should be invoked to account for the extravagance of sexually selected characters. The "Fisher index" is a useful indicator of the importance of the Fisher process in models and data. ... To believe in the Fisher-Lande process as an explanation of sexual selection without abundant proof is methodologically wicked, and I know of no relevant evidence at all. Such a belief inhibits the search for patterns which might disprove it. The main implication of the handicap principle for present purposes is that sexually selected ornaments have meanings which are worth discovering, and forms which can be explained; and that the key to both is their cost. (p. 487)[6]

In light of the above statements culled directly from the sexual selection literature therefore, it is far from clear that sensory/cognitive bias explanations can provide a complete

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[6] Like Grafen (1990), Iwasa, Pomiankowski, & Nee (1991) also highlight the fluid relationship between the various evolutionary processes of sexual selection (i.e., runaway and good genes).

explanation of sexually-selected traits *even* in instances where Fisherian runaway selection via sensory bias originally caused the focal trait to start evolving, and progressively elaborated it over evolutionary time. If such a trait crossed a threshold whereby it henceforth became a highly condition-dependent indicator of fitness, it could theoretically have been hijacked by good genes sexual selection. As such, both the trait itself and the preference for it could thereby be further altered or extended by good genes sexual selection for their new fitness-enhancing roles. Relatedly, it is also worth noting that Kokko (2001) cautions that good genes sexual selection can in fact occur even when males being selected for their good genes survive on average for a shorter time than other males with genes of lesser quality. In the human case, one might here analogously imagine some predisposition to an earlier death in those who produce especially costly mating displays in some signaling channel. Hypothetically speaking, the ancestral fitness benefits, perhaps in the form of increased offspring, may have paid the costs of earlier death resulting from such intense signaling.

Tangentially but interestingly, some researchers have also examined and found evidence for traits evincing use for both intra-sexual competition and inter-sexual signaling (Berglund, Bisazza, & Pilastro, 1996). This "armament-ornament" model also points to the fact that a condition-dependent armament used in intra-sexual competition can subsequently and additionally take on the function of acting as a condition-dependent ornament in mating. In other words, because such an armament evolved as an honest signal in male-male competition, used by males to assess the combat ability of their conspecifics, females of a species can also then come to capitalize on the same signal, thus allowing them to preferentially mate with males in possession of good genes. The central idea here is that the armament also acts a proxy for fitness, given its condition-dependent nature, and so becomes a signal that females can benefit from by

tracking and using to discriminate the genetic quality of males—which of course entails that females must also evolve preferences for such traits. Moreover, this consequent co-opting can also act on the trait and elaborate it further, ceteris paribus. To take one concrete empirical example, Griggio, Serra, Licheri, Monti, and Pilastro (2007) found evidence for this "armament-ornament" view in their study of rock sparrows, whereby carotenoid-based pigment in the male plumage functioned as a competitive signal amongst males and also as a signal preferred by females in mate choice. Incidentally, the carotenoid-based signal also functioned as a mate choice preference of males when selecting females, too, showing that mate choice for good genes indicators can be reciprocal—that it can act to sculpt traits in both males in females, as in Miller's theory of human cognitive evolution.

Sexually-selected indicators and adaptations

As applied to human cognitive evolution, looking for signs of sexually-selected adaptations likely requires employing criteria that differs in some respects from more standard adaptationist criteria. In the hands of evolutionary psychologists, standard adaptationist criteria more or less holds that adaptations exhibit the following properties: (1) high efficiency, (2) high complexity, (3) high modularity, (4) low phenotypic variance, (5) low genotypic variance, (6) low heritability, (7) cross-cultural universality (or commonality), (8) universality across time, (9) species-typical development, and (10) functional design conducive to fitness under ancestral conditions, if not also currently (Miller, 2000c). Such criteria are also best viewed as a cluster-class, whereby not all adaptations need satisfy each property. Crucially, however, when posing hypotheses regarding sexually-selected indicator traits, some of these criteria are not applicable.

Firstly, with respect to efficiency, sexually-selected indicator traits tend to be quite inefficient. Secondly, the complexity of a signal designed to be broadcast to potential mates may also appear relatively simplistic when taken in isolation. However, when seen in the context of the wider signaling game and/or system of which it is an integral part, it may be seen to be quite complex after all. Perceivers often evolve complex capacities to appraise the merits of sexually-selected indicators, and therefore much of a signal's complexity can rely on the implicit meaning embedded in the appraisal mechanisms of the perceiver. As such, when investigating for signs of sexual selection one should bear this in mind and examine signals as they are embedded in the wider signaling game and system in which they function. Thirdly, with respect to modularity, because fitness indicators evolve to be reliable indices of underlying phenotypic and genotypic fitness, they reflect all of the constituent modular components that are tributary to a given indicator in question. For if indicator traits arose from simply one or two cognitive modules they would cease to be a particularly informative and reliable indicator of an organism's overall fitness. Thus, sexual selection forges indicators that tend to tap a broad array of modular components, which in turn vouchsafes their reliability as indices of fitness.

Fourthly, the criteria of low phenotypic and genotypic variance, as well as heritability, are also problematic with respect to sexually-selected indicators. Unlike universal, species-typical adaptations, which tend to exhibit low phenotypic and genotypic variances and low heritability, sexually-selected indicators exhibit the converse: high levels of phenotypic and genotypic variance and high heritability. There has been a tendency in the past for researchers to mistake traits evincing such high phenotypic and genotypic variances and high heritability for mere evolutionary noise. So a sexual selection perspective, at the very least, poses questions that otherwise might remain invisible under the assumption that such traits represent neutral,

evolutionary noise. Fifthly, with respect to the criterion of cross-cultural universality—and as with the case of species-typical cognitive adaptations more generally—one must be careful not to mistake highly variable concrete instantiations for an absence of an underlying adaptation. That is to say, one must be careful not to restrict their investigation to the surface-level features of those instantiations of the indicator signal, lest one miss the underlying logic and structure undergirding that *type* of indicator signal.

To illustrate this point, consider linguistic facility deployed in the mating domain—that is, in the service of mating effort. If, for argument's sake, some aspects of language production and comprehension evolved in humans via sexual selection as an indicator signal and appraisal capacity, respectively, it would be methodologically misguided to exclusively confine one's attention to the surface-level features of that signal channel which ostensibly vary across cultures—i.e., phonemes, words, etc. Instead, one would want to probe deeper to see if there might be an underlying structure to the signal—a structure which may be obfuscated by the variable surface-level instantiations. Indeed, the conflation of surface-level instantiations with deeper-level cognitive structures and processes, the latter of which may have been sculpted by selection for some specific purpose(s), and that therefore may be undergirding those surface-level instantiations in patterned ways, need similarly be avoided.[7]

To take another example, if music production is similarly a capacity that has been at least partly shaped by sexual selection, it would follow that culturally variable expressions of that capacity—e.g., jazz, hip hop, playing percussion instruments, opera singing—are *token*

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[7] Analogously, Dickins and Rahman (2012) point out that work on soft inheritance—i.e., transgenerational epigenetics, cultural transmission, and niche construction—overlooks the possibility that such processes could very well have deeper rationales, and hence a "deeper structure" undergirding the variable surface level phenomena, that were directly selected for by evolution.

instantiations of a more general, fundamental *type* whose ultimate rationale has been "endorsed", so to speak, by sexual selection. The token instantiations would therefore be multiple ways of reliably indicating music producers' underlying fitness. Moreover, the exact form that the token instantiations would take would be both constrained by the cognitive architecture undergirding their genesis, as well as culturally-contingent. It might therefore be expected that the cultural emergence of the token signals would arise through a bi-directional, dynamic interplay between humans' postulated cognitive architecture for such a sexually-selected display capacity, on the one hand, and whatever the manifold of contingent cultural, social, and other environmental facts obtaining locally happens to be, on the other hand. The evolved cognitive basis therefore guides and constrains the general shape of what token signals can take, and the relevant contingent sociocultural and ecological facts flesh out the surface-level details within those species-typical parameters set by the underlying type (as governed by the underlying sexually-selected cognitive adaptation). One general upshot to this sketch is that the emergence and stabilization of the various tokens of musical expression would come to characterize the various culturally-local "mating games" that individuals can partake in. De Block and Dewitte (2007) have discussed various hypothetical characteristics of mating games, and how they might function as display niches locally within cultures. Hypothetically speaking, the set of possible mating display signals which are evolutionarily stable should, at minimum, all possess the common property of being costly signals, and as such function as reliable indicators of phenotypic condition and genotypic quality.

Sexually-selected fitness indicators: creativity and humor as a case study

In light of the discussion of exaptation and adaptation, there would appear to be another theoretically possible route through which fitness indicators may have evolved: initially via Fisherian runaway selection, by tapping into cognitive or perceptual biases that were pre-existent in conspecifics and which caused those conspecifics to prefer certain traits during courtship, and with those indicator traits in turn becoming progressively elaborated over evolutionary time. A preference for humor, for example, might possibly have arisen, at least initially, as a by-product of other cognitive adaptations—by somehow cognitively biasing mate choosers to exhibit a preference for humorous mates. Humor production may then have been progressively elaborated through the Fisherian runaway process. Hypothetically speaking, therefore, the capacity for humor production may originally have arisen as a response to a cognitive bias in perceivers.

For our purposes it is not so important to flesh out any specific historical account. Rather, the key upshot here is that humor capacity could eventually come to act as a fitness indicator insofar as it became an honest and reliable indicator of phenotypic condition and genetic quality. The corollary to this conclusion—and an important one to bear in mind—is that the overall hypothesis does not therefore become falsified if one has good reason to believe that some postulated sexually-selected indicator trait had its evolution initially, or even mainly, powered by Fisherian runaway selection. For, to reiterate, once a given trait crosses some condition-dependent threshold, males or females of the species would henceforth be selecting mates on the basis of good genes.

Empirically speaking, several studies have shown a positive relationship between IQ and body symmetry, the latter of which, as noted, is taken to be a measure of developmental stability, and hence an index of underlying genetic quality (e.g., Prokosch, Yeo, & Miller, 2005; but see Johnson, Segal, & Bouchard, 2008). Indeed, evidence also indicates a positive relationship

between body asymmetry and atypical brain asymmetries (Yeo, Gangestad, & Thoma, 2007).

Various lines of evidence also support Miller's theory more directly, at the level of overt

behavior. For instance, partial support in favor of the hypothesis that art functions as a fitness

indicator signaled in mating contexts was found by Clegg, Nettle, and Miell (2011). In their

particular sample of artists, successful male artists had more sexual partners than less successful

artists. An analysis performed by Kanazawa (2000) was also consistent with the sexual selection

hypothesis that scientific production functions partly as an evolutionarily-novel expression of an

evolved mating disposition for cultural display.

More crucially, perhaps, some psychometric evidence supports the existence of a link

between creativity and general intelligence (Nusbaum and Silvia 2011; Kaufman, Kozbelt,

Bromley, & Miller, 2008). Significantly, a recent study found that the number and size of rare

copy number variations (CNVs)—specifically, deletions in chromosomal segments of the

genome, and the total nucleotide length of such deletions—predicted reduced intelligence in

those subjects identified as possessing such deletions (Yeo, Gangestad, Liu, Calhoun, &

Hutchison, 2011). Since CNVs are the result of mutation and hence contribute to overall

mutation load, and which furthermore had a significant and negative effect on intelligence in the

subjects of Yeo et al. (2011), it is fully consistent with the hypothesis that cognitive traits

function as fitness indicators, in virtue of g indexing mutation load, as the study of Yeo et al.

(2011) confirms. Indeed, that intelligence would be sensitive to overall mutation load in this way

is of course precisely what the theory proposed by Miller (2001) predicts.

In a series of evolutionarily-framed studies of mating cognition, Griskevicius, Cialdini,

and Kenrick (2006) found that experimentally-induced mating primes evoked creativity in

predictable ways in both men and women. And Haselton and Miller (2006) predicted and found

that women's short-term mating preferences for creativity in males increased with their propinquity to ovulation (ovulation being, of course, when conception occurs, hence precisely when women can benefit from securing good genes for their offspring). However, the reported findings of Haselton and Miller (2006) can be interpreted differently on the basis of the empirical results of Prokosch, Coss, Scheib, and Blozis (2009). According to these results, women's preferences for creative displays in men may not vary as a function of menstrual cycle phase, however the creative displays may themselves still function simultaneously as both good genes indicators and good partner and good provider indicators. If something like this latter scenario is accurate, it may have been selectively disadvantageous for women to have evolved shifting preferences for creativity that were mediated by menstrual cycle phase, whereby creativity would be preferred less during the infertile, luteal phase. Such a state of affairs may instead have exerted a selection pressure on women to track the creativity of men across their menstrual cycle: primarily as a good genes indicator when in the fertile phase of the cycle, and primarily as a good provider indicator when in the infertile phase of the cycle.

Picciuto and Carruthers (in press) argue for an account of the origins of creativity that is explicitly open to this broader "dual benefits" possibility. As such, their explanatory framework leaves open the possibility that creative displays act both as good genes indicators, on the one hand, and good partner indicators, on the other. More specifically, however, their particular account sees the capacity for creativity as being first cultivated in childhood via pretend play.[8] They contend that a more fully-developed capacity for creativity, in turn, facilitates later problem-solving in adulthood (see also Carruthers, 2002). Such an account is therefore

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[8] The account of Picciuto and Carruthers (in press) has much in common with the view that animal play early in ontogeny helps develops the survival skills that are to be employed later in life (see Allen & Bekoff, 1999, Ch. 6).

supportive, for instance, of the view that creative displays in mating contexts may act as a good provider indicator in men, if not also a good partner indicator as well. Cast in more ancestral terms, the thought here is that creative display acts as a proxy for, say, hunting and foraging ability and parenting skills, and that it therefore might behoove women to select as long-term mates males evincing an especially creative disposition, which in turn augurs successful provisioning and parenting. A similar account could equally apply to creativity in women, mutatis mutandis. Alternatively, sexual selection might potentially enhance a trait such as creativity, though not because the enhanced levels of the trait per se index a lower mutation load, but rather because the enhanced trait levels also serve as good partner indicators (either in one or both of the sexes). A variant of this hypothesis is that perhaps creativity does not serve as a good genes indicator at all, but rather can be accounted for largely or entirely by dint of sexual selection. And as always, sexual selection can shape any given trait in either a sexually dimorphic way or in both sexes—and a trait in one sex may not be the result of direct selection at all, but rather as a correlated outcome of Fisherian runaway selection, whereby a trait and the preference for it become linked within both sexes.

Prima facie, it is perhaps possible that certain alleles are maintained in the gene pool because they give rise to especially creative cognitive and behavioral tendencies when found in the genotype of individuals who also possess relatively high intelligence, and thus lower mutation loads. Wilkins and Godfrey-Smith (2009) provide a discussion of how such *balancing-selection* scenarios can play out over evolutionary time, with balancing-selection referring to the process by which multiple alleles at a given genetic locus can be maintained in a gene pool by selection if those alleles differ in their fitness values across a range of different contexts (i.e., temporal, spatial, genetic). Specifically in this case, balancing-selection would hypothetically

emerge against the backdrop of the differing possible genotypes that make up the genetic contexts that creativity-boosting alleles might find themselves in. Perhaps sexual selection was constrained by the pre-existing genetic architecture of the brain, and hence the only way genetic variants could generate highly creative displays—and concomitantly highly attractive ones—was by causing obligate effects in cognition whose fitness effects were rather diametrically opposed, depending on the individual in which those alleles express themselves: highly creative and hence attractive cognition in individuals whose genotypes are characterized by lower mutation load (higher intelligence) on the one hand, and evincing psychopathologies or sub-clinical symptoms in those individuals whose genotypes are characterized by higher mutation load (lower intelligence) on the other hand. In other words, such creativity-boosting alleles would cause fitness decrements when found in individuals of low intelligence, but fitness benefits—presumably in terms of more or higher quality mates—when found in individuals of high intelligence.

Indeed, there is evidence that decreased *latent disinhibition*, which gives rise to cognitive phenomena such as defocused attention, and in general much less sub-conscious "filtering" of irrelevant information and stimuli, combines with general intelligence in such a way to permit highly creative cognition (Carson, Higgins, & Peterson, 2003). When possessing decreased latent disinhibition, those also in possession of higher intelligence are much better able to both combine disparate elements into novel and interesting ideas and vet them before they are given expression. The various forms of analogical thinking, divergent thinking, and broad associational cognition, inter alia, that latent disinhibition permits, show signs of being in part explained by some specific biological and molecular-genetic underpinnings, and confer psychopathology in individuals with low intelligence (Carson, 2011). Keller and Miller (2006) argued that polygenic

mutation selection-balance best explains the evolutionary persistence of common, harmful, heritable mental disorders, and such a view is seemingly concordant with the possibility that creativity-boosting alleles, when finding themselves in the genotypes of individuals high in mutation load, will contribute to the symptomatology of various psychopathologies (e.g., schizophrenia).

The hypothetical requirement of additional genetic variants in addition to high general intelligence for highly creative cognition is corroborated by evidence showing that the Creative Achievement Questionnaire—an instrument demonstrating good reliability, validity, internal consistency, and convergent validity—strongly and accurately predicted creative achievement (including humor) across various studies in a variety of domains, even independent of IQ (Carson, Peterson, & Higgins, 2005). Shaner, Miller, and Mintz (2004) proposed that modifier alleles may in fact act as amplifiers that boost the sensitivity of some specific sexually-selected indicator trait—perhaps, for example, some facet of verbal courtship—to an individual's underlying genetic quality and condition. As such, individuals with low mutation loads and hence higher intelligence, who also possess the amplifying modifier alleles, would broadcast the indicator trait in highly attractive ways. Shaner et al. (2004) also suggest that schizophrenia, in particular, is the low fitness extreme of such a sexually-selected fitness indicator.

Interestingly, Shaner et al. (2004) additionally argue that such a model has much explanatory power and makes a number of key predictions, and that different modifier alleles might be found across different human populations, with perhaps specific alleles that are less sensitive to underlying mutation load and condition being found among populations (or individuals derived from such populations) with lower levels of sexual competition and reproductive variance, and those specific alleles that are more sensitive to underlying mutation

load and condition being found among populations (or individuals derived from such populations) with higher levels of sexual competition and reproductive variance (i.e., populations characterized by high degrees of polygyny or high degrees of infidelity). It is also possible that some other adaptive scenarios might explain possible differences in the distribution of such hypothetical modifier alleles. In addition, the Big Five traits of openness and extraversion have been shown to increase creativity among individuals when combined with higher intelligence (Peterson, Smith, & Carson, 2002; Miller & Tal, 2007). So perhaps the polymorphisms (gene variants) that enhance creativity are associated in particular with openness and extraversion.

At the level of neurobiology, Ramachandran and Hubbard (2001) have hypothesized that various types of synaesthesia are caused by various cross-wirings occurring within the fusiform and angular gyri, and have also likewise hypothesized that neural hyperconnnectivity and cross-wiring between disparate brain regions might at least partially underlie creative cognition. Ramachandran and Hubbard (2001) argue that this possibility is in line with the fact that synaesthesia has a higher incidence among artists and poets. Brang and Ramachandran (2008) have suggested that the HTR2A gene—which is implicated in serotonin receptor activation— plays an important role in the genesis of synaesthesia. Hence, if it is true that specific polymorphisms can cause forms of synaesthesia-mediated creative cognition, then perhaps it and/or various other polymorphisms at specific genetic loci have been selected and maintained in the gene pool for their effects on other forms of creative cognition—and perhaps via the hyperconnectivity patterns and neural cross-wiring that Ramachandran and Hubbard (2001) suggest.

Finally, with respect to humor, Bressler and Balshine (2006) found that women subjects preferred humorous men as relationship partners. Howrigan and MacDonald (2008) also found

subjects' general intelligence to correlate positively with their humor production ability, as judged by observers. Replicating this result, Greengross and Miller (2011) found that humor ability both reveals intelligence and predicts mating success. Both Howrigan and MacDonald's (2008) and Greengross and Miller's (2011) results are particularly interesting, since they provide empirical support for precisely the sort of predictions that Miller's theory makes with respect to a trait such as humor. Furthermore, both men and women highly value a sense of humor in a mate (Buss, 2003). It should be noted, however, that humor is one specific form of creativity. As such, some forms of creativity might hypothetically have been subjected to sexual selection, while other forms—i.e., discovery and invention—might hypothetically have been subjected to other forms of natural selection.

Conclusion

To briefly recapitulate the foregoing, we have seen how heritable variation in fitness generated by mutation-selection balance opens the door for sexual selection to potentially evolve fitness indicators and mating preferences for them. We have also seen how a cluster of interrelated concepts, namely costly signaling, condition-dependence, mutation target size, and mutation-selection balance, function in the overall theory advanced by Miller (2001) that various human cognitive capacities have evolved via sexual selection to function as fitness indicators. It was argued that the *g*-factor of general intelligence comprises a substantial subset of an *f*-factor of overall fitness, that the *g*-factor is hence an excellent candidate for serving as a window onto the overall mutation load of an individual, and that it might accordingly mediate the expression of sexually-selected traits such as creativity. Traits like creativity, therefore, would hypothetically serve to broadcast an individual's underlying genetic and phenotypic quality.

It was argued that conceptual subtleties relevant to the relation between exaptation and adaptation, on the one hand, and Fisherian runaway selection and good genes sexual selection, on the other, are integral to understanding the processes by which traits might hypothetically evolve to function as fitness indicators. Specifically, we have seen the way in which traits which evolved for other purposes may potentially become exapted and then adaptively altered or extended by sexual selection for a new or additional function as fitness indicators. And we have seen how Fisherian runaway selection or sensory/cognitive biases can drive the evolution of traits to an extent that transforms them into highly condition-dependent traits, and hence legitimate candidates for use as good genes fitness indicators. Finally, various conceptual and methodological criteria of relevance to investigating and identifying sexually-selected adaptations were outlined, followed by a brief look at empirical work that has aimed to test whether humor and creativity more generally function as fitness indicators.

A research program aiming to investigate the hypothesis that creative displays or humor production function as fitness indicators would do well to examine further their psychometric properties, and elucidate the extent to which they are subserved by general intelligence. Neurobiological investigation of the basis of creative cognition might also prove illuminating in this regard. If however the link between creativity or humor and the g-factor turns out to be minimal or tenuous at best, a (perhaps distant) future molecular-genetic understanding of the cognitive neurobiology of both capacities might unveil the degree to which the mutation load underlying relevant brain areas is correlated with their degraded capacity. Such an alternative scenario might perhaps still indicate that humor production is serving as a fitness indicator in courtship. Another key research area for assessing potential indicator traits would be to give closer scrutiny to their potential cognitive and behavioral design features. Uncovering such

design features would enable potential inferences of adaptive function, as per reverse-engineering (Dennett, 1995, 1990; Lewens, 2004, 2002). The underlying cognitive basis of sexually-selected fitness indicators can be examined both in their signaling and assessment aspects, including the manner in which fitness cues, both physical and cognitive, might be individually weighted and integrated by mate choosers assessing potential mates (Miller & Todd, 1998; Miller, 1997b). It is also worth mentioning briefly the issue of possible sexual dimorphism in the expression of hypothetical indicator traits. Indeed, due to the fact that men stand to increase their reproductive fitness through having multiple offspring with many sexual partners, it is theoretically expected that they will be more indiscriminate in their broadcasting of good genes indicators such as creativity and humor. Women, on the other hand, would be expected to more narrowly convey such traits, mainly to those suitors who they assess to be good long-term relationship prospects, in an attempt to gain their commitment.

The aim of this paper has been to examine the central facet of the overall account advanced by Miller (2001), namely that cognitive traits can function as fitness indicators in the biologist's sense. To this end, the core theoretical foundations of the account were explored. Apart from this task of providing a coherent integration of the theory's foundational bases, some of the conceptual subtleties of exaptation, Fisherian runaway selection, and good genes sexual selection, all of which bear crucially on the overall theory, were analyzed. Candidate indicator traits such as creativity and humor were then considered in light of the theoretical core of the theory and its conceptual subtleties. The various lines of evidence available thus far support the theory. In sum, Miller's account appears to possess a reasonable degree of overall plausibility and deserves further empirical research.

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