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Approaches to an Evolutionary Personality Psychology:

The Case of Sociosexuality

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This thesis is dedicated to my son Richard.

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Abstract

Evolutionary approaches have not been as successful in personality psychology as they were in other areas of psychology, arguably because of the misfit between modern evolutionary psychology's strong focus on universal adaptations and the study of (mostly heritable) individual differences in personality psychology. In this thesis, two alternative evolutionary approaches, which appear more suitable for personality psychology, are discussed and applied. The *evolutionary genetic approach* asks why genetic variance in personality differences exists. In the first part of this thesis, three evolutionary genetic mechanisms that could explain genetic variance in personality differences are assessed: selective neutrality, mutation-selection balance, and balancing selection. Based on evolutionary genetic theory and empirical results from behavior genetics and personality psychology, it is concluded that selective neutrality is largely irrelevant, that mutation-selection balance seems best at explaining genetic variance in intelligence, and that balancing selection by environmental heterogeneity seems best at explaining genetic variance in personality traits. A general model of heritable personality differences is presented, which conceptualizes intelligence as a fitness component and personality traits as individual reaction norms of genotypes across environments, with different fitness consequences in different environmental niches. Complementary to the evolutionary genetic approach, the *life history approach* starts with how people allocate their resources to evolutionarily relevant life tasks. It asks how individual differences in these allocation decisions emerge from the interplay of various developmental components, including personality differences. In the second part of this thesis, differences in the allocation to long-term versus short-term mating tactics (as reflected in the construct of sociosexuality) are used as a case to exemplify this approach. Two new measures for the assessment of sociosexuality components are presented. While the revised Sociosexual Orientation Inventory (SOI-R) is a questionnaire that assesses the facets Behavior, Attitude and Desire, the sociosexuality Single-Attribute Implicit Association Test (SA-IAT) is a new methodic development aimed to assess implicit sociosexuality indirectly. Both measures showed concurrent validity in online studies, but only the SOI-R facets were predictive of mating tactics, including observed flirting behavior, as well as for the number of sexual partners and changes in romantic relationship status over the following 12 months. Furthermore, distinct sex differences, developmental trends, degrees of assortative mating, and effects on a romantic partner were found for the three SOI-R facets, indicating their unique roles in the development of mating tactics.

Zusammenfassung

Evolutionäre Herangehensweisen hatten in der Persönlichkeitspsychologie nicht den gleichen Erfolg wie in anderen Bereichen der Psychologie, vermutlich wegen der Fehlpassung des starken Fokus auf universelle Adaptationen in der modernen Evolutionspsychologie mit der Untersuchung (größtenteils erblicher) individueller Unterschiede in der Persönlichkeitspsychologie. In dieser Dissertationsschrift werden zwei alternative evolutionäre Herangehensweisen diskutiert und angewendet, welche passender für die Persönlichkeitspsychologie erscheinen. Die *evolutionsgenetische Herangehensweise* fragt, warum genetische Varianz in Persönlichkeitsunterschieden existiert. Im ersten Teil dieser Dissertationsschrift werden verschiedene evolutionsgenetische Mechanismen, die genetische Varianz erklären können, verglichen. Auf Grundlage evolutionsgenetischer Theorie und empirischen Befunden aus der Verhaltensgenetik und Persönlichkeitspsychologie wird geschlussfolgert, dass ein Mutations-Selektions-Gleichgewicht genetische Varianz in Intelligenzunterschieden gut erklären kann, während ausgleichende Selektion durch Umweltheterogenität die plausibelste Erklärung für genetische Unterschiede in Persönlichkeitseigenschaften ist. Es wird ein allgemeines Modell vorgeschlagen, welches Intelligenz als Fitnesskomponente konzeptualisiert und Persönlichkeitseigenschaften als individuelle Reaktionsnormen von Genotypen auffasst, welche unterschiedliche Fitnesskonsequenzen in unterschiedlichen Umweltnischen haben. Komplementär zur evolutionsgenetischen Herangehensweise beginnt die *„Life History"-Herangehensweise* damit, wie Menschen ihre Ressourcen in evolutionär relevante Lebensbereiche investieren. Sie fragt, wie Unterschiede in diesen Investitionsentscheidungen aus dem Zusammenspiel verschiedener Entwicklungsomponenten entstehen, einschließlich Persönlichkeitsunterschiede. Im zweiten Teil der Dissertationsschrift wird diese Herangehensweise am Beispiel von Investitionsunterschieden in Langzeit- versus Kurzzeit-Paarungstaktiken (wie im Konstrukt der Soziosexualität abgebildet) erläutert. Zwei neue Maße zur Erfassung von Soziosexualitätskomponenten werden vorgestellt. Während das revidierte Soziosexuelle Orientierungsinventar (SOI-R) ein Fragebogen zur Erfassung der Facetten „bisheriges Verhalten", „Einstellung" und „Begehren" ist, wurde mit dem „Single-Attribute" Impliziten Assoziationstest (SA-IAT) eine neue Methode zur indirekten Erfassung impliziter Soziosexualität entwickelt. Beide Maße zeigten konkurrente Validität in Onlinestudien, aber nur die SOI-R-Facetten erwiesen sich als prädiktiv für Paarungstaktiken, einschließlich beobachtetem Flirtverhalten sowie der Zahl der Sexualpartner und Veränderungen im Beziehungsstatus innerhalb der nächsten 12 Monate. Weiterhin wurden für die SOI-R-Facetten distinkte Geschlechtsunterschiede, Entwicklungsverläufe, Grade selektiver Partnerwahl, und Effekte auf den Beziehungspartner gefunden, was ihre spezifischen Rollen in der Entwicklung von Paarungstaktiken unterstreicht.

Introduction

Over the last two decades, evolutionary approaches had a great deal of success in various branches of psychology (e.g. Buss, 2005; Dunbar & Barrett, 2007). However, personality psychology apparently withstands this general trend. While some notable theoretical attempts toward an evolutionary personality psychology have been made as early as 1990 (Buss, 1990; Tooby & Cosmides, 1990), not much has happened since then, and the current state must be regarded as unsatisfactory (Miller, 2000; Nettle, 2006). An evolutionary account for personality differences is generally acknowledged as a valuable goal for personality psychology in the long run (e.g. McAdams & Pals, 2006), but evolutionary approaches have clearly not pervaded mainstream personality research. The overarching goal of this thesis is to provide and exemplify evolutionary approaches that are suitable for personality research.

One of the main reasons for the low impact that evolutionary psychology had on personality research is likely that modern evolutionary psychology has focused very much on adaptations. *Adaptationistic evolutionary psychology* studies domain-specific solutions to reoccurring adaptive problems in the universal design of the human species. A defining characteristic of these adaptations is that they have been fixed in the human genome, which means that they show no genetic variation. They are inherited, but not heritable (Tooby & Cosmides, 1990, 2005). This severely limits the value of the adaptationistic approach to personality research: while it can be used to explain sex differences (Mealey, 2000) and some individual differences resulting from conditional developmental reactions to environmental factors (e.g. attachment styles, e.g. Buss & Greiling, 1999), it is unable to explain heritable individual differences (Tooby & Cosmides, 1990) – and a heritable component has been established for virtually all personality differences (Plomin, DeFries, McClearn & McGuffin, 2001; Turkheimer, 2000).

Alternative to the adaptationistic approach, an evolutionary genetic approach can explain genetic differences between individuals from an evolutionary perspective. E*volutionary genetics* studies the effects of processes like mutation, selection, genetic drift, and migration on genetic variation between individuals and across populations (Maynard Smith, 1998; Roff, 1997).In the first part of this thesis, comprised by the theoretical target article “The evolutionary genetics of personality” (Penke, Denissen & Miller, in press a), 22 peer commentaries, and the author’s reply (Penke, Denissen & Miller, in press b), it is argued that evolutionary genetics provides a more suitable approach to personality psychology than adaptationism. While some evolutionary genetic mechanisms have already been alluded to in earlier evolutionary treatises on personality (Buss, 1990, 1991; MacDonald, 1995; Nettle, 2006; Tooby & Cosmides, 1990), these articles have not exploited the full potential of an evolutionary genetic approach. Penke et al. (in press a, b) argue that the degree of

elaboration of modern evolutionary genetic models and the wealth of data on human personality allows us to infer which evolutionary genetic mechanisms are most plausibly responsible for the existence and maintenance of genetic variation in personality differences. They conclude that a small set of evolutionarily independent dimensions of genetic personality differences exist in humans, of which the one underlying the *g* factor of intelligence is most likely maintained by a balance of new mutation and counteracting selection, while those underlying broad personality domains (as for example represented in the Five Factor Model of personality) most likely still exist because spatial or temporal heterogeneity in our (physical and social) environment causes balanced selection pressures on them. Penke et al. (in press a, b) also provide insights into how an evolutionary perspective might help to understand the complex interplay between genes and environmental factors in producing personality phenotypes.

Evolutionary genetics thus offers a “bottom-up” approach to an evolutionary personality psychology, one where the genetic level is linked to individual differences in abstract behavioral dispositions (i.e., personality traits and abilities). However, such dispositions can only be evolutionarily relevant if they translate into consequential behaviors. More specifically, they have to influence how well people are able to extract resources (ultimately energy) from their environments, and how they invest these resources into conflicting life domains of evolutionary relevance (i.e., growth, survival, reproduction, and the support of genetic relatives). These potentials and allocation decisions, which influence reproductive success and ultimately fitness, are studied in evolutionary anthropology and behavioral ecology within the framework of life history theory (Kaplan & Gangestad, 2005). The *life history approach* thus deals with individual differences in highly complex behavioral and developmental strategies and tactics for the allocation of resources across the lifespan. Life history strategies and tactics can be conceptualized as the final outcome of (1) interacting systems of adaptations (Kaplan & Gangestad, 2005, 2007; White, Dill & Crawford, 2007), which are often sensitive to an individual’s own potential (i.e., condition) and to the environment (e.g. Gangestad & Simpson, 2000), and (2) genetic differences within these systems (Roff, 2002). However, the step from broad and complex strategies and tactics to domain-specific adaptations and genetic differences is a big one - from the very “downstream” to the very “upstream” in terms of the watershed model that Penke et al. (in press a) adopted from Cannon and Keller (2005). Therefore, it might be worthwhile (if not necessary) to take an intermediate step and start with studying the mid-level components of life-history strategies and tactics, as well as their interactions with each other and with relevant environmental factors across the lifespan. Since these mid-level developmental components include personality differences (both heritable and environmental-contingent), life history theory offers a “top-down” approach to an evolutionary personality psychology.

The life history approach is thus complementary to the evolutionary genetic “bottom-up” approach: While the former connects personality to fitness, the latter connects genes to personality.

The second part of this thesis uses the life history trade-off between long-term and short-term mating tactics as an exemplary case for the life history approach to personality. Long-term mating tactics include developing and protecting an exclusive and committedromantic relationship, usually accompanied by high levels of parental investment in potential offspring. In contrast, short-term mating tactics include investing greater efforts in finding and courting potential mates, in order to have sexual affairs with either many mates or mates of especially high quality. Individual differences along this dimension of mating tactics are often equated with sociosexual orientations, which describes individual differences in the willingness to have uncommitted sex (Simpson et al., 2004). Both papers in the second part of this thesis were aimed to contribute to a dissection of this broad life history trait into its mid-level components.

Penke and Asendorpf (2007) developed a revised version of the Sociosexual Orientation Inventory (SOI; Simpson & Gangestad, 1991), a short self-report questionnaire which is the most established measure of sociosexuality. The new SOI-R assesses three facets of global sociosexuality (desire, attitude, and past behavioral experiences). Penke, Eichstaedt and Asendorpf (2006) deviated from the usual reliance on self-reports and attempted to develop an indirect measure of implicit sociosexuality. This latter work was inspired by the recent trend in social psychology to explain behavior as the outcome of two different cognitive systems, distinguished by their reliance on automatic versus reflective information processing. It has been argued that the automatic systems is more involved in the generation of spontaneous, impulsive behavior, while the reflective system is responsible for deliberate behavior (Strack & Deutsch, 2004). Since Implicit Association Tests (IATs) are assumed to be capable of assessing individual differences in implicit personality self-concepts (Schnabel, Greenwald & Asendorpf, in press), and have indeed shown incremental validity over explicit self-report measures in the prediction of spontaneous behavior in some studies (e.g. Asendorpf, Banse & Mücke, 2002), Penke et al. (2006) developed a variant of the IAT procedure, the Single-Attribute IAT (SA-IAT), for the assessment of implicit sociosexuality. The rationale here was that if some of the psychological components that influence mating tactics operate on the automatic level, they might be better captured by an indirect measure like the sociosexuality SA-IAT than by an explicit self-repot measure like the SOI or SOI-R. (Note that, while Barrett, Frederick, Haselton and Kurzban, 2006, recently argued that evolved psychological mechanisms do not *have* to operate at the automatic level, it is possible that some of them do. Characterizing the level of operation for psychological adaptations might help us to understand them better.)

Both the SOI-R facets and the sociosexuality SA-IAT showed promising concurrent validities in cross-sectional online studies (Penke et al., 2006, Study 2; Penke & Asendorpf, 2007, Study 1). However, while the SOI-R facets (especially desire and past behavioral experiences) predicted future behavioral expressions of mating tactics, including flirting behavior towards an opposite-sex stranger, changes in romantic relationship status, and the number of sexual partners during the next 12 months (Penke & Asendorpf, 2007, Study 2), the SA-IAT showed no significant relationships with any of these criteria (all *p*s > .10) (Penke & Asendorpf, 2006; these SA-IAT results are not reported in the article). Furthermore, while Penke and Asendorpf (2007) found a highly differentiated pattern of sex differences, effects on romantic partners, personality-relationship transactions, and assortative mating for the three SOI-R facets, none of these effects could be established for the SA-IAT (all *p*s > .10; not reported in the article). Thus, while the data suggests that sociosexual desires, attitudes and past behavioral experiences (as measured by the SOI-R) belong to the mid-level components that interact during development to form a life history pattern of mating tactics, no evidence was found for an implicit sociosexuality component.

However, this does not necessarily imply that there are no implicit aspects of sociosexuality that influence mating behavior. Indeed, some lines of evidence suggest that a methodological issue of the SA-IAT was at least partly responsible for its failure to predict behavioural outcomes: First, the internal consistency of the SA-IAT was much lower in the lab study reported in Penke and Asendorpf (2007), where the behavioral criteria were assessed, than in the internet study reported in Penke et al. (2006) (Cronbach's $\alpha = .82$ vs. .66 in the lab and online study, respectively). Second, during the follow-up study of the lab sample (see Penke & Asendorpf, 2007), the participants completed an online version of exactly the same SA-IAT they completed during the lab session one year earlier (not reported in the article). When done at home, the SA-IAT had a higher consistency ($\alpha = .74$) within the same sample of subjects. Furthermore, the participants showed shorter average reaction latencies ($t_{(217)} = 5.07$, $p < .001$, $d = .22$) and made more errors in the central classification task ($t_{(217)} = 9.70$, $p < .001$, $d = .60$) when doing the SA-IAT at home compared to the lab (where the SA-IAT was the very first task after an initial "icebreaker" test). Given that the SA-IAT procedure is simpler and more transparent than the traditional IAT procedure, one interpretation of this pattern of findings is that the SA-IAT is too easy, and can be completed as a simple reaction task that is unaffected by implicit associations if subjects are very concentrated and motivated to solve the classification task correctly (Penke & Asendorpf, 2006). Future studies might be able to develop more robust and reliable measures of implicit sociosexuality, and it remains to be seen how these measures fare in the prediction of behavioral outcomes before a firm conclusion can be drawn about the cognitive level on which sociosexuality-related psychological mechanisms operate.

To summarize, evolutionary genetics and life history theory offer complementary evolutionary approaches to personality psychology. Both approaches do not suffer from mainstream evolutionary psychology's narrow focus on human universals, but explicitly address individual differences. Taken together, they provide a potent framework for an evolutionary personality psychology.

While this thesis sketches and exemplifies how such an evolutionary personality psychology might look like, it cannot be considered as a comprehensive treatment of the topic. Even for the case of sociosexuality, only first steps are taken. For example, few is known about the genetic underpinnings of sociosexuality. The only behavior genetic study explicitly concerned with sociosexuality (Bailey, Kirk, Zhu, Dunne & Martin, 2000) used a modified version of the SOI, which put a strong accent on the attitudinal component, and thus likely changed its focus. Penke and Asendorpf (2007) found that heritable personality traits like shyness and sensation seeking are related to various sociosexuality components. They thus likely influence the individual development of mating tactics over the lifespan. Evolutionary models of human mating have predicted that the same environmental factors that affect how people allocate their resources to short-term versus long-term mating tactics (like the harshness of living conditions; Gangestad & Simpson, 2000) also exert selection pressures on genetic polymorphisms that are related to these personality traits (like the DRD4 variants; Harpending & Cochran, 2002). This thesis can only suggest loose links between the different levels. It remains a subject for future studies to determine how exactly universal adaptations, heritable personality traits, and environmental factors influence which life history strategies and tactics individuals develop over their lifespan.

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Part I:

The Evolutionary Genetic Approach

The evolutionary genetics of personality

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Abstract

Genetic influences on personality differences are ubiquitous, but their nature is not well understood. A theoretical framework might help, and can be provided by evolutionary genetics. We assess three evolutionary genetic mechanisms that could explain genetic variance in personality differences: selective neutrality, mutation-selection balance, and balancing selection. Based on evolutionary genetic theory and empirical results from behaviour genetics and personality psychology, we conclude that selective neutrality is largely irrelevant, that mutation-selection balance seems best at explaining genetic variance in intelligence, and that balancing selection by environmental heterogeneity seems best at explaining genetic variance in personality traits. We propose a general model of heritable personality differences that conceptualises intelligence as a fitness component and personality traits as individual reaction norms of genotypes across environments, with different fitness consequences in different environmental niches. We also discuss the place of mental health in the model. This evolutionary genetic framework highlights the role of gene-environment interactions in the study of personality, yields new insight into the person-situation-debate and the structure of personality, and has practical implications for both quantitative and molecular genetic studies of personality.

Evolutionary thinking has a long history in psychology (e.g. James, 1890; McDougall, 1908; Thorndike, 1909). However, the new wave of evolutionary psychology (e.g. Buss, 1995; Tooby & Cosmides, 2005) has focused almost exclusively on human universals – the complex psychological adaptations that became genetically fixed throughout our species due to natural selection (Andrews, Gangestad & Matthews, 2002) and that should therefore show zero genetic variation and zero heritability (Tooby & Cosmides, 1990). In sharp contrast, one of personality psychology's most important findings in the last three decades has been that virtually every aspect of personality is heritable (Plomin, DeFries, McClearn & Mc Guffin, 2001). This fact is now so well established that Turkheimer (2000; Turkheimer & Gottesman, 1991) even called it a law. The mismatch between evolutionary psychology's adaptationist focus on human universals and the omnipresence of heritable variance in human personality might explain why early approaches towards an evolutionary personality psychology (Buss, 1991; Tooby & Cosmides, 1990; MacDonald, 1995, 1998) remained rather unsatisfactory (see Miller, 2000a; Nettle, 2006a). On the other hand, traditional behaviour genetics did not explain the evolutionary origins and persistence of genetic variation in personality, and sometimes even viewed genetic variation in traits as evidence of their evolutionary irrelevance. Thus, the evolutionary psychology of human universals and the behaviour genetics of personality differences share a biological metatheory, but had almost no influence on each other (Tooby & Cosmides, 1990, 2005; Plomin et al., 2001).

We believe that this mutual neglect has been unfortunate for both fields, and has especially harmed the development of an integrative evolutionary personality psychology. Evolutionary studies of species-typical universals and individual differences were already successfully merged during the 'Modern Synthesis' in the 1930s, when Sir Ronald A. Fisher, Sewell Wright, J. B. S. Haldane, and others united the branches of biology that were founded by the cousins Charles Darwin (the father of adaptationism) and Sir Francis Galton (the father of psychometrics and behaviour genetics) (Mayr, 1993). These 1930s biologists created what is now known as 'evolutionary genetics', which deals with the origins, maintenance, and implications of natural genetic variation in traits across individuals and species. Evolutionary genetics mathematically models the effects of mutation, selection, migration, and drift on the genetic basis of traits in populations (Roff, 1997, Maynard Smith, 1998). In the following, we will argue that personality psychology needs an evolutionary genetic perspective in order to draw maximal benefits from behaviour genetic findings and the evolutionary metatheory. This is important, since understanding the evolutionary behaviour genetics of personality is fundamental to the future development of a more unified personality psychology (McAdams & Pals, 2006).

Overview

The central topic of this review is how evolutionary genetics can inform our theoretical understanding of heritable personality differences and their genetic foundations. We use 'personality differences' in the broad European sense of encompassing individual differences in both cognitive abilities and personality traits (e.g. Eysenck & Eysenck, 1985). Cognitive abilities reflect an individual's maximal performance in solving cognitive tasks. It is well-established that a single continuum of general intelligence (*g*), ranging from mild mental retardation to giftedness, explains a large proportion of the individual differences in cognitive abilities across domains (Jensen, 1998), especially on genetic level (Plomin & Spinath, 2004). Our discussion on cognitive abilities will be focused on this general intelligence dimension. Personality traits reflect an individual's set of typical behavioural tendencies exhibited in situations that leave room for diverse adaptive responses. The myriad of personality trait dimensions are usually organized in structural models. Broad personality trait domains, as in the Five Factor Model of personality (FFM), are generally regarded as stable and temperamental in nature (John & Srivastava, 1999). They are what we mean by 'personality traits'.

We argue that the classical distinction between cognitive abilities and personality traits is much more than just a historical convention or a methodological matter of different measurement approaches (see Cronbach, 1949), and instead reflects different kinds of selection pressures that have shaped distinctive genetic architectures for these two classes of personality differences. In order to make this argument, we will first give a brief introduction to the nature of genetic variation and the major mechanisms that contemporary evolutionary genetics proposes for its maintenance in populations. After this, we will critically review earlier evolutionary approaches to personality and clarify the role of environmental influences within this approach. This will culminate in an integrative model of the evolutionary genetics of personality differences, including new, theory-based definitions of cognitive abilities and personality traits, as well as a discussion of how common psychopathologies (such as schizophrenia and psychopathy) may fit into an evolutionary genetic model of personality differences. Finally, we will discuss this model's implications for an integrated evolutionary personality psychology grounded in both behaviour genetics and evolutionary genetics.

What is Genetic Variation? Most personality psychologists now accept Turkheimer's (2000) first law of behaviour genetics ('everything is heritable'). Yet how does systematic genetic variation in personality traits arise? A complete understanding of the insights offered by evolutionary genetics requires a brief review of some of the basics of genetics and evolutionary theory, which we provide in the following.

The human genome. The human genome consists of about 3.2 billion base pairs that are unequally spread across 24 distinct chromosomes. Only about 75 million (2.3%) of these base pairs are organized in roughly 25,000 genes (i.e. regions or 'loci' translated into actual protein structures); the rest (traditionally called 'junk DNA') do not code for proteins, but may play important roles in gene regulation and expression (Shapiro & von Sternberg, 2005). On average, any two same-sex individuals randomly drawn from the total human population are 99.9% identical with regard to their base pairs (Human Genome Project, 2001), even though genomic identity is somewhat further attenuated by copy-number variations (CNVs, individual differences in the repetitions of DNA segments) (Redon et al., 2006). This species-typical genome contains the universal human heritage that ensures the highly reliable ontogenetic reoccurrence of the complex functional human design across generations ('design reincarnation', Barrett, 2006; Tooby, Cosmides & Barrett, 2005). Adaptationistic evolutionary approaches usually care only about this universal part of the genome and its species-typical phenotypic products (Andrews et al., 2002; Tooby & Cosmides, 2005).

Mutation. During an individual lifespan, the genome is passed from mother cells to daughter cells by self-replication, and if this results in a germline (sperm or egg) cell, half of the genome eventually ends up combining with an opposite-sex germline cell during sexual reproduction, and is thus passed from parent to offspring. While genomic self-replication is astonishingly precise, it is not perfect. Replication errors can occur in the form of point mutations (substituting one of the four possible nucleotides in a base pair for another one, also referred to as *single nucleotide polymorphisms* (*SNPs*)), CNVs (duplications or deletions of base pair sequences), or rearrangements of larger chromosomal regions (e.g. translocations, inversions). All of these copying errors are referred to as *mutations*, and they are ultimately the only possible source of genetic variation between individuals. Recent scans of whole human genotypes reported 9.2 million candidate SNPs (International HapMap Consortium, 2005) and 1,447 candidate CNV regions (Redon et al., 2006).

Sexual reproduction endows an individual with a unique mixture of their parents' genotypes. In the short term, this process of sexual recombination is the major cause of genetic individuality. In the evolutionary long term, however, sexual recombination is less important, since it just reshuffles the parental genetic variation that was once caused by mutation. By convention, mutations that continue to be passed on to subsequent generations and that reach an arbitrary threshold of more than 1% prevalence in a population are called '*alleles'*. Since all alleles are mutations, we regard this distinction as hardly helpful. In contrast, '*polymorphism'* is a more neutral term for genetic variants that can be at any prevalence. In order to highlight the evolutionary genetic perspective, we will use the terms 'mutation' and 'polymorphism' interchangeably.

Some mutations are phenotypically neutral, often because they do not affect protein structure or gene regulation. Most mutations in protein-coding and genomic regulatory regions, however, tend to be harmful to the organism because they randomly disrupt the evolved genetic information, thereby eroding the complex phenotypic functional design (Ridley, 2000; Tooby & Cosmides, 1990). Only very rarely does a random mutation improve the functional efficiency of an existing adaptation in relation to its environment, which is more likely if the environment has changed since the adaptation evolved (Brcic-Kostic, 2005). Deletions, insertions, and larger rearrangements of base pair sequences tend to have quite strong disruptive effects on the phenotype, often leading to prenatal death or severe birth defects. Point mutations (SNPs) and duplication-type CNVs (see Hurles, 2004), on the other hand, can have phenotypic effects of any strength, including quite mild effects, and it is likely that they are the most common source of genetic variation between individuals.

Behaviour genetics. Quantitative traits, such as intelligence and personality traits, are polygenic - they are affected by many mutations at many genetic loci, each of which is called a quantitative trait locus (QTL) (Plomin, Owen & McGuffin, 1994). *Quantitative behaviour genetics* basically compares trait similarities across individuals that systemically differ in the genetic or environmental influences they have in common (e.g. identical vs. fraternal twins, adoptive vs. biological children), to decompose the variation of quantitative traits, and their covariances with other traits, into genetic and environmental (co)variance components. It also tries to estimate how much of the genetic (co)variance is due to 'additive effects' of QTLs (which allow traits to 'breed true' from parents to offspring) versus interactions between alleles at the same genetic locus ('dominance effects') or across different genetic loci ('epistatic effects'). Dominance and epistatic effects lead to non-additive genetic variance (V_{NA}) between individuals, as opposed to the additive genetic variance (V_A) caused by additive effects. Together with the environmental variance (V_E) and gene-environment (GxE) interactions, these components determine the phenotypic variance (V_P) that we can observe in personality differences. In contrast to quantitative behaviour genetics, *molecular behaviour genetics* uses so-called 'linkage' and 'association' methods to directly analyse human DNA variation in relation to personality variation, to identify the specific QTLs that influence particular trait (co)variations (Plomin et al., 2001).

Natural Selection. Mutations in functional regions of the genome provide half of the basic ingredients for biological evolution. The other half is natural selection, which is the differential reproduction of the resulting phenotypes (Darwin, 1859). Any mutation that affects the phenotype is potentially visible to natural selection, though to varying degrees. Of course, those rare mutations that actually increase fitness will tend to spread through the population, driving adaptive evolution. Selection is most obvious against mutations that lead to premature death or sterility. Such mutations are eliminated from the population within one

generation, and can only be reintroduced by new mutations at the same genetic loci. Mutations with less severe effects tend to persist in the population for some time; they are selected out of the population more quickly when their additive effect reduces the *fitness* of the genotype (i.e., its statistical propensity for successful reproduction) more severely. This relationship between the additive phenotypic effect of a genetic variant and its likely persistence in a population is described by the *fundamental theorem of natural selection* (Fisher, 1930).

To summarize, any genetic variation in any human trait is ultimately the result of mutational change in functional regions of the species-typical genome. Natural selection counteracts disruptive changes by eliminating harmful mutations from the population, at a rate proportional to the mutation's additive genetic reduction in fitness. Only mutations that affect the organism's fitness in a positive or neutral way can spread in the population and will reach the 1% prevalence of an 'allele'. Most psychological traits, including personality differences, are complex in design and continuously variable across individuals, indicating that many polymorphisms at many loci are responsible for their genetic variation.

Why is There Genetic Variation in Personality?

Also else being equal, it seems plausible that natural selection should favour an invariant, species-typical genome that codes for a single optimal phenotype with optimal fitness. In other words, evolution should eliminate genetic variation in all traits, including all aspects of personality. So how can personality differences still be heritable (i.e., genetically variable) after all these generations of evolution? To answer this fundamental question, an evolutionary genetic approach to personality is needed.

With the growing acceptance of evolution as a metatheory for psychology, more and more personality psychologists are trying to conceptualize personality in an evolutionary framework. Unfortunately, these good intentions seldom lead to more than an affirmation that certain heritable dimensions are part of our evolved human nature (e.g. McCrae & Costa, 1996; Ashton & Lee, 2001; McAdams & Pals, 2006). Even worse, some conceptualisations of human cognitive abilities ignore genetic variation completely and discuss these heritable, variable traits as if they were invariant adaptations (e.g. Cosmides & Tooby, 2002; Kanazawa, 2004). Other authors (Goldberg, 1981; Buss, 1990; Hogan, 1996; Ellis, Simpson & Campbell, 2002) take genetic variation in personality differences for granted, and try to understand evolved features of our 'person perception system' that explain why we categorize others along these dimensions. Few have attempted an evolutionary genetic approach to explain the persistence of heritable variation in personality itself.

Evolutionary genetics offers a variety of mechanisms that could explain persistent genetic variation in personality differences. These mechanisms include *selective neutrality*

(where mutations are invisible to selection), *mutation-selection balance* (where selection counteracts mutations, but is unable to eliminate all of them), and *balancing selection* (where selection itself maintains genetic variation). Recent theoretical developments make it possible to predict how each of these mechanisms would influence certain genetic and phenotypic features of traits (see Table 1). Conversely, if these features are known for a given trait, it is possible to identify which evolutionary processes likely maintained the genetic variants that underlie its heritability. We will now review existing attempts to explain personality differences from an evolutionary perspective, and evaluate them in the light of modern evolutionary genetics.

Insert Table 1 about here

Can Selective Neutrality Explain Genetic Variance in Personality?

Tooby and Cosmides (1990) developed an early and highly influential perspective on the evolutionary genetics of personality. They reviewed the state of evolutionary genetics at that time, but, as major advocates of an adaptationistic evolutionary psychology, they focused on species-typical psychological adaptations and downplayed genetic variation as minor evolutionary noise. In their view, one plausible mechanism that could maintain genetic variation in psychological differences is selective neutrality (Kimura, 1983). This occurs when fitness-neutral mutations (that have no net effect on survival or reproductive success, averaged across all relevant environments) accumulate to increase genetic variance in a trait. For example, the exact route that the small intestine takes within one's abdomen may have little influence on digestive efficiency, so neutral genetic variation that influences patterns of gut-packing could easily accumulate. In the evolutionary short-term, selective neutrality allows genetic variance in traits to increase.

However, what happens in the evolutionary long-term to selectively neutral traits? Since neutral mutations are, by definition, unaffected by natural selection, the only evolutionary force that can affect neutral genetic variation is genetic drift – and drift always tends to decrease genetic variance. Drift is basically the fixation (to 100% prevalence) or elimination (to 0% prevalence) of a polymorphism by chance. There is only one factor that is known to be important for the efficacy of drift: it is stronger when the 'effective population size' (N_e) (the average number of reproductively active individuals in a population) is smaller (Lynch & Hill, 1986). What is really critical for the effect of genetic drift is the minimum N_e during occasional harsh conditions (e.g. ice ages, disease pandemics) that created 'genetic bottlenecks' (especially small effective population sizes). In humans, 10,000 seems to be a good estimate for the minimum N_e (Cargill et al., 1999). Mathematical models show that, with such a relatively large N_e, drift is fairly weak and selective neutrality could, in principle, account for almost all genetic variance in any human trait (Lynch & Hill, 1986).

So far, so good: perhaps most genetic variation in human personality is due to selective neutrality – maybe there is no average net fitness cost or benefit to being extraverted versus introverted, or agreeable versus egoistic. However, the critical assumption for selective neutrality is that genetic drift is more important than natural selection in affecting a trait's genetic variance. This is only the case if the selection coefficient *s* is less than about $1/4N_e$ (Keller & Miller, 2006a). Thus, the larger the effective population size, the harder it is for a trait to be selectively neutral. Given the reasonably large estimate of minimum human N_e from above (10,000), a typical human trait is selectively neutral only if the average net fitness of individuals with a certain polymorphism is between 99.997 and 100.003% of the average fitness of individuals without that polymorphism (Keller & Miller, 2006a). For example, an allele that influences extraversion would be truly neutral only if extraverts had, not just the same number of 1st-generation offspring as introverts, but (almost) exactly the same average number of 15th generation descendants (great[13] grandchildren). In addition, this finely-balanced neutrality must hold across all relevant environments: if there are some environments in which outgoing, risk-seeking extraverts do better, and other environments in which shy, risk-averse introverts do better (a GxE interaction), then extraversion would be under balancing selection (see below), not selective neutrality.

This makes selective neutrality an implausible explanation for heritable personality differences, because human personality traits influence outcomes in all areas of life (Ozer & Benet-Martinez, 2006), including such obviously fitness-relevant aspects as health (Neeleman, Sytema & Wadsworth, 2002), life expectancy (Friedman et al., 1995), mating strategies (Nettle, 2005), and reproductive success (Eaves et al., 1990). Indeed, similar non-neutral relationships between personality and fitness have been observed in various other species (Dingemanse & Réale, 2005). The relation between cognitive abilities and fitness components has also been impressively demonstrated by Gottfredson (2004, in press), Deary (e.g. Deary et al., 2004; Deary & Der, 2005), and Miller (2000b; Prokosch, Yeo & Miller, 2005).

How could we tell if a heritable individual difference was the outcome of selective neutrality? Typically, selective neutrality leads to a distinct structure of genetic variation in quantitative traits (such as personality differences). If a mutation affects the phenotypic expression of a trait, it will first of all have a main effect, which means it will contribute to the additive genetic variance (V_A) of the trait. Only if the mutation happens to interact with other polymorphisms (at the same or other loci, through dominance or epistasis, respectively), will it contributes to the non-additive genetic variance (V_{NA}) of the trait. This is exactly the same logic that holds for any statistical analysis: ceteris paribus, main effects are much more likely than interaction effects. Since all else is equal under selective neutrality by definition, we can

expect low absolute values of V_{NA} for any selectively neutral trait (Lynch & Hill, 1986; Merilä & Sheldon, 1999), and a very small proportion of non-additive genetic variance (D_α), defined by Crnokrak and Roff (1995) as:

$$D_\alpha = V_{NA} / (V_{NA} + {}_{VA})$$

Traits with a recent history of selection, by contrast, should show a significant absolute and proportional amount of V_{NA} (Crnokrak & Roff, 1995; Merilä & Sheldon, 1999; Stirling, Réale & Roff, 2002). This follows from Fisher's (1930) fundamental theorem of natural selection: since V_A is passed directly from parents to offspring, it will be reduced very quickly by natural selection for any non-neutral trait. V_{NA}, on the other hand, is affected much more weakly by selection, since the interacting genetic components that constitute the V_{NA} are continuously broken apart by sexual recombination and thus not passed from parents to offspring. As a result, a high proportion of V_{NA} in a trait would argue against the trait's selective neutrality. There is now strong evidence that personality traits show substantial V_{NA} (Eaves et al., 1998; Keller et al., 2005) - including some initial molecular evidence for epistatic interactions (Strobel et al., 2003) – which suggests they are not selectively neutral. In contrast, cognitive abilities seem to show less V_{NA} (Chipuer, Rovine & Plomin, 1990), a point we consider later.

As summarized in Table 1, genetic variation persists in populations through selective neutrality only if its phenotypic consequences are (almost) completely unrelated to fitness in any environment. This genetic variation can be expected to be mainly additive. While it is possible that this holds for some relatively trivial traits (e.g. gut-packing design), it is highly implausible for major personality differences, given their pervasive effects on social, sexual, and familial life.

Can Mutation-Selection Balance Explain Genetic Variance in Personality?

Mutation rates and mutation load. As stated previously, a truly neutral trait has to show a close-to-null relationship to any fitness component in any environment. All traits that do not fulfil this very strict requirement are subject to natural selection. As long as the direction of selection is relatively constant, Fisher's (1930) fundamental theorem predicts that the additive genetic variance of the trait will be reduced to the point where one genetic variant becomes fixed as a universal, species-typical adaptation. The rate of reduction in a trait's genetic variance is influenced by two factors with opposing effects: the mutation rate (which increases genetic variance) and the strength of selection (which decreases genetic variance). The mutation rate tells us how fast new mutations are introduced into functional parts of the genome (i.e., protein-coding genes and their regulatory regions). Comparative molecular genetic studies suggest that humans have a comparatively high mutation rate (Eyre-Walker & Keightley, 1999), with the best available estimate being an average of about

1.67 new mutations per individual per generation (Keightley & Gaffney, 2003). Given reasonable assumptions about mutations arising in a Poisson frequency distribution, one can calculate that the probability of a human being born without any new mutations is slightly lower than one in five (Keller, in press). Importantly, this estimate includes only *non-neutral* mutations (polymorphisms that are visible to selection). As argued above, almost all non-neutral mutations tend to be harmful, and selection is stronger against more harmful mutations. For example, a mutation that reduces number of surviving offspring by 1% will persist for an average of ten generations in a large population, passing through the genotypes of about 100 individuals during that time. A mutation with a weaker 0.1% fitness reduction (which is still ten times stronger than selective neutrality in humans) will persist for four generations longer, afflicting about 1,000 individuals (Garcia-Dorado, Caballero & Crow, 2003). Because harmful mutations with dominant effects are an easier target for selection, only recessive mutations are likely to persist for a longer time (Zhang & Hill, 2005).

It follows that there is a *mutation load* of older, mildly harmful, and mostly recessive mutations in any individual at any point in time. This mutation load is mostly inherited from parents to offspring, but a few new mutations arise in each generation. Thus, each particular mutation will be eliminated by selection eventually, but at the same time new mutations will arise. According to very conservative estimates, the average number of mildly harmful mutations carried by humans is about 500 (Fay, Wyckoff & Wu, 2001; Sunyaev et al., 2001) and the standard deviation is 22 (or higher, given assortative mating, as we discuss below) (Keller & Miller, 2006a). This mutation load may account for a substantial portion of genetic variance in many fitness-related traits – perhaps including personality differences.

Mutational target size. For a long time, Fisher's fundamental theorem was thought to imply that traits that affect fitness more strongly should show less V_A (Falconer, 1981). In the early 1990s, however, Price and Schluter (1991) and Houle (1992) showed that the reverse is true: more fitness-related traits actually tend to have *higher* V_A. The reason that this could remain unnoticed for more than half a century was that evolutionary geneticists used to standardize additive genetic variance (V_A) by the total phenotypic variance (V_P) of the trait, yielding its narrow-sense heritability (h^2):

$$h^2 = V_A / V_P$$

Insofar as heritability was taken as a rough proxy for additive genetic variance, this gives profoundly misleading results, because V_P contains both the non-additive genetic (V_{NA}) and the environmental variance (V_E). Even if V_A is large, h^2 can be small when V_{NA} and/or V_E are even larger. Since V_E is especially population- and trait-specific, h^2 is not very informative for comparing genetic variances. Houle (1992) instead proposed to use the 'coefficient of

additive genetic variation' (CV_A) for comparisons across traits, populations, and species. It is defined as:

$$C_{VA} = [\mathrm{sqrt}(V_A) / M] * 100$$

or, equivalently,

$$C_{VA} = [\mathrm{sqrt}(V_P * h^2) / M] * 100$$

with M being the phenotypic trait mean and 100 a conventional scaling-factor. The CV_A thus standardizes V_A by the mean of the trait, whereas h^2 standardizes V_A by its total phenotypic variance. As long as all traits are measured on a ratio scale and some basic scaling effects are taken into account (Stirling et al., 2002), CV_As are directly comparable across traits and species, which does not hold for h^2s. For many traits across many species, it turned out that V_A increases with the fitness-relevance of a trait (Houle, 1992; Pomiankowski & Møller, 1995; Stirling et al., 2002). Because very high residual variances (V_{NA} + V_E) often overshadow substantial V_As, low h^2 values often fail to reflect this pattern (Rowe & Houle, 1996; Merilä & Sheldon, 1999; Stirling et al., 2002).

But how could the traits under strongest selection show the highest V_As? The key seems to be the number of genetic loci that could potentially disrupt the trait by mutating, which is called the *mutational target-size* of a trait (Houle, 1998). Since mutations occur with random probability at any genetic locus, the number of mutations that affect a trait (i.e., its mutation load) increases linearly with the number of genetic loci that affect the trait. Note that we are referring to the total number of genetic loci that could *potentially* affect the trait if they became polymorphic due to mutation, not the number of loci that are *actually* polymorphic at a given point in time (i.e., the QTLs), which are only about 10% of the potential loci (Pritchard, 2001; Rudan et al., 2003). Fisher's (1930) fundamental theorem works best for traits that are affected by only one genetic locus (Price, 1972; Ewens, 1989). The more genetic loci affect a trait, the greater the probability that any of these loci will be hit by a mutation, the more mutations will accumulate in the trait, and the harder it will be for selection to deplete the V_A of this trait. Instead of reaching genetic uniformity, non-neutral traits with large mutational target sizes will therefore be stuck in a balanced state of mutation and selection.

The trait with the largest mutational target-size is, of course, fitness itself: it is influenced by all selectively non-neutral parts of the genome (Houle et al., 1994). Fitness should therefore have a very large CV_A, which is in fact the case (Burt, 1995). Similarly, other traits closely related to fitness (e.g. so-called 'life history traits', such as longevity or total offspring number) are usually complex compounds of various heritable traits, leading to high mutational target sizes. For example, longevity is potentially influenced by disruptions in any

organ system – circulatory, nervous, endocrine, skeletal, etc. – so its mutational target size includes the mutational target sizes of all these organ systems. Consistent with this, very high CV_As have been reported for life-history traits in various species (Houle, 1992), including humans (Miller & Penke, 2007; Hughes & Burleson, 2000). In contrast, low CV_As can be found in genetically simpler traits less related to fitness, such as some morphological traits (e.g. bristle number in fruit flies or height in humans - Pomiankowski & Møller, 1995; Miller & Penke, 2007).

Insert Figure 1 about here

The watershed model. Cannon and Keller (2005; see also Keller & Miller, 2006a) introduced the *watershed model* (Figure 1) as an analogy to illustrate the relation between genetic variation and the mutational target size of traits. Its basic point is that 'downstream' traits, which are closely related to overall fitness, require the adaptive functioning of virtually the whole organism – the integrated functioning of many subsidiary 'upstream' mechanisms - behavioural, physiological, and morphological. Just as many small creeks join to become a stream, and several streams join to become a river, many genetic and neurophysiological micro-processes (e.g. the regulation of neural migration, axonal myelinization, and neurotransmitter levels) might interact to become a specific personality trait. These personality traits will interact to influence success in survival, socializing, attracting mates, and raising offspring – which in turn determines overall fitness. The upstream micro-processes, such as the regulation of a particular neurotransmitter, may be influenced by only a few genes. The broader middle-level processes, such as reactivity to social stress, are influenced by all genes that affect the corresponding upstream processes. The same holds true for even broader (i.e., more downstream) domains of organismic functioning – which are equivalent to broad components of fitness itself (e.g. sexual attractiveness, social status, foraging efficiency) – these depend on all of the genes that affect all of their upstream processes. A similar argument holds for environmental influences, which, when affecting upstream processes, accumulate in downstream traits. But because selection is much less effective in reducing V_E, the V_E of fitness components tends to be large, which reduces their heritability. Merilä and Sheldon (1999) argued that V_{NA} is as robust against selection as V_E, which would imply a high D_α for traits under mutation-selection balance. However, more recent evidence questions the robustness of V_{NA} to selection in downstream traits (Stirling et al., 2002). The exact expected size of D_α for traits under mutation-selection balance must thus be regarded an unresolved issue, though it is likely in the medium range.

Developmental stability and the f-factor. As an addition to the watershed model, developmental stability theory (Polak, 2003) explains how mutations that are spread across the genome influence fitness. It argues that organisms often fail to develop according to the evolved blueprint in their genome, since either the blueprint itself or the relevant

environmental factors are disrupted. In such a case, the evolved fit between genome and environment is disrupted. Whereas the genomic blueprint is disrupted by mutations, the organism's developmental environment can be disrupted by factors such as pathogens and toxins. From a fitness perspective, the exact combination of disruptive factors doesn't matter: what counts is the total reduction in phenotypic functionality due to developmental instability. Similarly, only the total mutational damage in the genome is what counts for natural selection. Which genetic sequences the mutations disrupt are largely unimportant – and likely different for each human being.

An established measure of developmental stability is the bilateral symmetry of body parts that show perfect symmetry at the average population level (e.g. ankle breadth or ear length), usually aggregated across many body parts. Even though this only taps into morphological developmental stability, body symmetry shows relations to all kinds of fitness components in various species (Møller, 1997), including humans (Gangestad & Yeo, 1997; Gangestad & Simpson, 2000). One well-replicated correlate of body symmetry is general intelligence (Prokosch et al., 2005; Luxen & Buunk, 2006; Bates, 2007). Thus, some genetic and environmental disruptions can apparently impair both cognitive and morphological development. The watershed metaphor breaks down a bit at this point, because it fails to reflect the fact that most mutations are *pleiotropic* in their effects (Marcus, 2004): each mutation will tend to disrupt several downstream traits. Those harmful effects will be positively intercorrelated in the affected downstream traits (not because the effects are positive, but because they are consistently negative). Therefore, pleiotropic mutations should lead to a 'positive manifold' of intercorrelations among the efficiencies of mid-level processes and of fitness components. In addition, intercorrelations between various processes may arise through developmental interdependence (van der Maas et al., 2006). According to Miller (2000c), this should allow the extraction of a 'general fitness factor' or '*f*-factor' that reflects (inverse) overall mutation load. Just as the *g*-factor of general intelligence (Jensen, 1998) is at the top of a multi-level hierarchy of intercorrelated cognitive abilities, *f* is at the top of a similar hierarchy of genetically intercorrelated upstream traits and processes. In fact, Miller and colleagues (2000c; Prokosch et al., 2005) argued that *g* is an important subfactor of *f*, reflecting the integrative functioning of the cognitive system. The V_A of *g* may therefore reflect the aggregate harmful effects of mutations at any of the thousands of genetic loci that affect our brain development and functioning, each of which decreases our cognitive abilities a tiny bit.

Further predictions. Every trait under mutation-selection balance has to be a downstream trait, with mutations occurring randomly across all of the loci that contribute to its mutational target size. It is very unlikely that any of these harmful mutations will ever reach an intermediate prevalence rate in the face of selection working against it (Turelli & Barton,

2004). The mutations that cause the V_A of more complex downstream traits will thus be numerous, but individually rare, evolutionarily transient, and phenotypically mild in their effects. As a consequence, they will be extremely hard to detect using standard molecular genetic methods (linkage and association studies), and they will be very unlikely to replicate across populations (because different evolutionarily transient mutations tend to affect different populations). Furthermore, since the sheer number of involved loci will impede selection's ability to deplete V_A, the magnitude of D_α for downstream traits will likely be in the medium range (Stirling et al., 2002). These predictions (see Table 1) are consistent with what is currently known about the genetic structure of *g* (Plomin, Kennedy & Craig, 2006; Plomin & Spinath, 2004). Enormous efforts to identify single genes of major effect underlying intelligence led to meagre success at best, and to the conclusion that a huge number of pleiotropic polymorphisms must be responsible for its genetic variation (Kovas & Plomin, 2006). The situation is different for personality traits, however, since good candidates for underlying polymorphisms have been identified (Ebstein, 2006), and most of these have intermediate prevalence rates (Kidd, 2006). In addition, the amount of V_{NA} found in personality traits is often as high as the V_A component (Eaves et al., 1998; Keller et al., 2005), indicating a large D_α of .50 or higher. These characteristics of personality traits cannot be explained by mutation-selection balance.

Since traits with a large mutational target size tend to be most affected by mutations that are both rare and recessive, the probability that two copies of the same mutation come together in a single individual and unleash their full deleterious potential is much higher when both parents are genetically related. This is called *inbreeding depression*. Its counterpart is called *heterosis* or *outbreeding elevation*, and occurs when pairings of recessive, deleterious mutations are broken up by sexual recombination in offspring of highly unrelated parents (e.g. parents from different ethnic groups). Due to the predicted genetic structure of traits under mutation-selection balance, we can expect them to show both inbreeding depression and heterosis effects (DeRose & Roff, 1999; Lynch & Walsh, 1998). Such evidence exists for intelligence (reviewed in Jensen, 1998), but is, to the best of our knowledge, absent for personality traits. For example, the offspring of cousin marriages tend to be less intelligent, but we do not know of any evidence that they tend to be more or less extraverted, conscientious, or agreeable than average.

Finally, the typically harmful effects of mutations lead to a clear prediction about the social perception of their phenotypic effects. Since a high mutation load disrupts an organism's functional integrity and ultimately fitness, it should lead to a less favourable social evaluation by those who are looking for a good sexual partner, friend, or ally. The mating context is most important here, because about half of a sexual partner's mutation load will be passed along to one's offspring (Keller, in press). Indeed, virtually all modern evolutionary

theories of mate choice argue that any phenotypic trait that reliably signals that a potential mate has a low mutation load will be sexually attractive (Keller, in press; Kokko, Brooks, Jennions & Morley, 2003; Miller, 2000b, c). In an influential paper, Rowe and Houle (1996) argued that sexual selection would drive the evolution of any sexually attractive trait towards higher reliability by making its expression more *condition-dependent*, that is more dependent upon (and revealing of) the overall phenotypic condition (e.g. health, vigour) of the organism. Condition is a trait with very large mutational target size, near the downstream end of the watershed model (Figure 1), and very closely related to fitness (Tomkins, Radwan, Kotiaho & Tregenza, 2004). A condition-dependent trait is thus affected by larger parts of the genome – it will actually 'move downstream', insofar as it becomes sensitive to the efficiency of a larger number of upstream processes. This can explain why, across species, morphological traits that are preferred in mate choice (e.g. the plumage of finches) tend to have much higher CV_A than morphological traits that are irrelevant for mate choice (e.g. bristle number in fruitflies) (Pomiankowski & Møller, 1995), and almost as high as extreme downstream traits such as longevity and fertility.

Since traits that reliably reveal genetic quality (low mutation load) and general phenotypic condition tend to be highly variable within each sex and highly attractive to the other sex, mating markets in socially monogamous species (such as humans) tend to be competitive. Each individual tries to attract the highest-quality mate who will reciprocate his or her interest. Given a period of mutual search in such a competitive mating market, socially monogamous couples tend to form that are closely matched on the average attractiveness level of their sexually attractive traits (Penke, Todd, Lenton & Fasolo, in press). This phenomenon, called *assortative mating* (Vandenberg, 1972), is a typical population-level outcome for traits that are under mutation-selection balance, but it is much less likely for traits that are less related to fitness. Mate preferences for higher intelligence, and assortative mating with respect to intelligence, are well-established phenomena in humans, as is the condition-dependent expression of intelligence (Miller, 2000c; Miller & Penke, 2007). In contrast, mate preferences for personality traits tend to be modest in size and variable across individuals (Figueredo, Sefcek & Jones, 2006). In addition, there is almost no assortative mating for personality traits (e.g. Vandenberg, 1972; Lykken & Tellegen, 1993; Eaves et al., 1999). Thus, mate preferences for personality traits show quite a different pattern than mate preferences for universally sought traits, such as intelligence, mental health, and physical attractiveness– which are all presumably condition-dependent and under mutation-selection balance.[1]

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[1] Another domain of heritable personality differences for which strong assortative mating exists are some social attitudes, like conservatism or religiosity (Lykken & Tellegen, 1993; Eaves et al., 1999). However, unlike the basic personality traits and abilities we treat in this article, these attitudes must be

To summarize, mutation-selection balance is a very plausible mechanism for maintaining genetic variation in traits that reflect the overall functional integrity of the organism, including general intelligence and general health. This is reflected in the following features: high additive genetic variation, an elusive molecular genetic basis, condition-dependence, inbreeding and outbreeding effects, strong mate preferences, and assortative mating (see Table 1). Personality traits do not match these features nearly as well, suggesting that mutation-selection balance may not account for much genetic variance in personality traits.

Can Balancing Selection Explain Genetic Variance in Personality?

In both selective neutrality and mutation-selection balance, genetic variation is maintained because selection is unable to deplete it – either because the variation is selectively neutral, or because too much new variation is continually reintroduced. A quite different mechanism is the maintenance of genetic variation by selection itself. This *only* works if the selective forces that act on a trait are balanced, which occurs when both extremes of the same trait dimension are favoured by selection to the same degree under different conditions. Such balancing selection can happen in a variety of ways.

Variants of balancing selection. One form of balancing selection is *overdominance* (also called heterozygous advantage), which occurs when individuals with different alleles at the same genetic locus have a higher fitness than individuals with two identical copies. Sickle-cell anaemia is a famous textbook case of overdominance, but other examples have rarely been found in nature (Endler, 1986) or in animal experiments (Maynard Smith, 1998). Also, it is now widely believed that overdominance is evolutionary unstable and thus an unlikely candidate for maintaining genetic variation, especially in the long-term (Roff, 1997; Keller & Miller, 2006a; Bürger, 2000).

Another form of balancing selection is *antagonistic pleiotropy*, which occurs when polymorphisms have a positive effect on one fitness-related trait and a negative effect on another (Roff, 1997; Hendrick, 1999). A special case is sexually antagonistic co-evolution, where genetic variants are under opposing selection pressures in men and women (Rice & Chippindale, 2001). Since selection will usually fix the polymorphism with the least total

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regarded as complex developmental outcomes of GxE interactions (Eaves et al., 1999, pp. 77-78). Another noteworthy difference between attitudes and fitness-related traits like intelligence and attractiveness is that there seems to be no universal consensus in either sex on the desired attitudes of an ideal mate. It is thus implausible that competitive mating market dynamics cause assortative mating for attitudes in a similar way as they do for fitness components. Instead, social homogamy (i.e., mate search within the own peer group that tends to share similar attitudes) and later dyadic assimilation appear to be more promising explanations.

fitness cost, antagonistic pleiotropy could only maintain genetic variation if the fitness costs of all alleles at such a locus are exactly equal (averaged across environments). In addition, all heterozygous allele combinations have to provide all phenotypic fitness benefits that would be provided by both corresponding homozygous combinations ('reversal of dominance', Curtisinger, Service & Prout, 1994; Hendrick, 1999). Furthermore, independent of the number of genetic loci that affect a quantitative trait, antagonistic pleiotropy can maintain genetic variation only at one genetic locus (or two in the case of sexually antagonistic co-evolution) per trait (Turelli & Barton, 2004). Due to these highly restrictive conditions, it is very unlikely that antagonistic pleiotropy plays a major role in maintaining genetic variation (Hendrick, 1999) – although the special case of sexually antagonistic co-evolution might contribute to sex differences in personality and some within-sex personality variation (Keller & Miller, 2006b).

A more likely variant of balancing selection is *environmental heterogeneity*. When a trait's effect on fitness varies across space or time, significant genetic variation can be maintained in populations (Roff, 1997), even in quantitative traits (Bürger, 2000; Turelli & Barton, 2004). A necessary requirement for this to happen is that spatial or temporal fluctuations in selection pressures must occur such that the trait's net fitness effects are nearly neutral when averaged across all relevant spatiotemporal environments. It is not enough for a trait to be neutral in some environments or during some periods, because selection is very efficient at favouring polymorphisms with higher average fitness outcomes across all relevant environments. Only a fully balanced effect of different alleles across space and time will work to maintain genetic variation.

A related type of balancing selection is called *frequency-dependent selection*. In this case, the spatiotemporal fluctuations in selection pressures usually occur in the social environment of the species, rather than the external physical environment. Frequency-dependent selection can only maintain genetic variations if it is *negative*, favouring traits as long as they are rare in frequency (Maynard Smith, 1998). (Positive frequency-dependence will drive polymorphisms to fixation through a runaway, winner-take-all effect.) The 'social environment' is used in a very broad sense here, and can include the ratio of cooperative partners to cheaters (Mealey, 1995), the ratio of males to females (Fisher, 1930), the distribution of intra- and interspecific competitors for limited resources in ecological niches, or even parasite-host relationships (which occurs when viruses, bacteria or other pathogenes are best adapted to exploit the most common host phenotypes - Garrigan & Hedrick, 2003). Mathematical models have shown that negative frequency-dependent selection in any of these ways is a viable way to maintain genetic variance (Bürger, 2005; Schneider, 2006).

Thus, environmental heterogeneity and negative frequency-dependent selection are good candidates for maintaining genetic variance by balancing selection, whereas

overdominance and antagonistic pleiotropy can work only in rare cases that meet very restrictive conditions. The bottom line is that balancing selection requires a set of varying selection pressures that favour different phenotypes under different conditions. These fluctuating selection pressures must be stronger than any other unidirectional selection pressures on the same trait that consistently favour a certain optimal trait level in every environment (Turelli & Barton, 2004). If this condition is met, balancing selection leads to two or more different phenotypes (or a continuum of phenotypes) with identical average fitness across environments. Since these phenotypes cannot be further optimized by selection, they are called *evolutionary stable strategies* (*ESSs*) (Maynard Smith, 1982).

Predictions. Balancing selection leads to some distinctive genetic patterns. Reoccurring periods of selection in different directions tend to deplete the V_A of affected traits and result in higher D_α than found for selectively neutral traits (Roff, 1997). D_α will also be higher for traits under balancing selection than for traits under mutation-selection balance, since the former maintains polymorphisms at fewer genetic loci than the latter (Kopp & Hermisson, 2006), and selection is more effective in depleting the V_A from fewer genetic loci (van Oers et al., 2005; Stirling et al., 2002). Furthermore, balancing selection can maintain alleles in a population at intermediate prevalences, while mutation-selection balance cannot (Turelli & Barton, 2004). These characteristics (as summarized in Table 1) make balancing selection a likely candidate for maintaining genetic variation in personality traits, although it is unlikely to explain persistent genetic variance in cognitive abilities.

Balancing selection and personality traits. When Tooby and Cosmides (1990) argued that heritable personality differences are basically evolutionary noise, they suggested that parasite-host co-evolution (Garrigan & Hedrick, 2003), a form of negative frequency-dependent selection, might explain the striking amount of evolutionary 'noise' in human behavioural traits better than selective neutrality. Nonetheless, the central message was the same for both evolutionary processes: since the heritable aspects of personality are random by-products of functionally superficial biochemical differences that exist - at best - to prevent our lives from parasites, studying personality differences from an evolutionary perspective is a big waste of time. However, as argued above, there is strong evidence that personality differences have direct effects on fitness. In addition, Keller and Miller (2006a) noted that, for parasite-host co-evolution to explain personality variation as a by-product, there would have to be a very high degree of overlap between genetic loci that affect immune system function and genetic loci that affect personality differences – which seems unlikely.

MacDonald (1995, 1998) made an important step away from Tooby and Cosmides' 'neutral personality assumption' by proposing that five independent behavioural systems under balancing selection explain the dimensions of the Five Factor Model of personality (FFM). While he regarded both extremes of each dimension as maladaptive, with stabilizing

selection working against them, he assumed that the relatively broad middle range of each personality dimension reflects equally viable behavioural strategies (i.e., ESSs). MacDonald (1998) also argued that the viability of these strategies should vary across environmental niches. Following MacDonald (1995, 1998), Nettle (2006a) developed more specific hypotheses about the potential fitness costs and benefits associated with each of the FFM dimensions. If these evolutionary cost-benefit trade-offs were exactly the same in every environment, they could maintain genetic variance only through antagonistic pleiotropy, which tends to be evolutionary unstable. However, if the relevant selection pressures fluctuate across time or space, favouring different optima on the cost-benefit curves, they could maintain the range of viable personality trait levels. For example, Nettle (2006a) argued that high extraversion yields fitness benefits by promoting mating success, social alliance formation, and environmental exploration, but at the cost of increased physical risks and decreased romantic relationship stability. When environments are physically riskier to oneself and one's offspring (who benefit from relationship stability), high extraversion may be a net fitness cost; but when conditions are safer, high extraversion may yield a net fitness benefit. Environmental fluctuations would thus maintain genetic variation in extraversion.

The challenge in any such balancing selection argument is to identify the specific costs and benefits relevant to each personality trait across different environments. Originally, Nettle (2005) also hypothesized that extraverts might conserve energy by investing less parental effort in offspring, but failed to find supportive evidence. In fact, Nettle's list of extraversion costs and benefits might still be too long, with some proving to be fitness-irrelevant by-products. On the other hand, these are only some of the plausible costs and benefits. Different ones can be suggested for this and other personality traits (Denissen & Penke, 2006). Even if balancing selection proves a good general account of heritable personality traits, much more research would be needed to identify each personality trait's relevant fitness costs and benefits across different environments.

Environmental niches for personality traits. Recently, Camperio Ciani and colleagues (Camperio Ciani, Veronese, Capiluppi & Sartori, 2007) reported an interesting natural experiment that indirectly supports a role for balancing selection by environmental heterogeneity in sustaining the genetic variance of personality traits. They studied average personality differences on the FFM dimensions of Italian coast-dwellers compared to Italians living off the coast on three small island groups. After matching populations for cultural, historical and linguistic background, and controlling for age, sex and education, they found that individuals from families that have lived on small islands for at least 20 generations were lower in extraversion and openness to experience than both mainlanders and more recent immigrants to the island. This pattern makes cultural or developmental explanations for the population differences unlikely - it suggests change on the genetic level. Even though

individual fitness consequences of these traits were not measured directly, the apparent recent evolution of genetic differences between populations in these two traits suggests that the fitness payoffs of these two personality traits were historically distinct in these different environments.

In non-human species, recent studies suggest that environmental heterogeneity does impose varying selection pressures on personality traits. Dingenmanse, Both, Drent and Tinbergen (2004) could directly measure the fitness payoffs of personality differences (on a carefully assessed shyness-boldness dimension) in the great tit (*parus major*), which varied with food availability across breeding seasons. Similar evidence of environmental heterogeneity favouring personalities exists for some other species (reviewed in Dingenmanse & Réale, 2005).

More direct evidence for the importance of environmental heterogeneity in the evolutionary genetics of human personality comes from studies of the global distribution of polymorphisms at the DRD4 locus. This gene regulates dopamine receptors in the brain and has been associated with personality traits such as novelty seeking and extraversion (Ebstein, 2006). The prevalences of different DRD4 alleles differ dramatically across world regions. The evolutionarily newer 7R allele, which is more common in risk-prone, response-ready, extraverted novelty seekers, is much more prevalent in European and American populations than in Asian populations (Chang et al., 1996). This allele appears to be favoured by selection (1) when benefits can be gained from migrating to new environments (Chen et al., 1999; Ding et al., 2002), and (2) under resource-rich environmental conditions (Wang et al., 2004). Referring to these findings, Harpending and Cochran (2002) noted that under conditions of environmental harshness and resource scarcity (as is common in hunter-gatherer societies), intensive cooperation, strong family ties, stable pair bonds, and biparental investment are necessary for survival and successful reproduction. These ancestrally typical conditions would maintain the more risk-averse, ancestral form of the DRD4 gene. But under more luxuriant environmental conditions, when children can survive without so much paternal support (as in most agricultural and modern societies), the more risk-seeking 7R allele should be favoured by selection, as it leads to a personality more prone to sexual promiscuity and intrasexual competition (see also Gangestad & Simpson, 2000; Schmitt, 2005).

Arguments for frequency-dependent selection. The role of competition demands some more attention here. Competition, whether for mates, food, or other limited resources, is often a zero-sum game: The winner gains a benefit, but the loser usually pays a cost, at least in the form of wasted time and effort. As the competition within a niche becomes more intense, selection may eventually favour less competitive individuals who refrain from seeking these benefits to avoid the associated costs. This is the logic of the so-called ‘hawk-

dove game', the classic example of negative frequency-dependent selection (Maynard Smith, 1982). In fact, some evolutionary geneticists have argued that most environmental niches are actually social in nature, because the fluctuating selection regimes caused by environmental heterogeneity are almost always mediated by within-species competition that often takes the form of negative frequency-dependent selection (Bürger, 2005; Kassen, 2002). It is interesting in this regard that personality differences have been found almost exclusively in social species (Figueredo et al., 2005a) and that they tend to have stronger effects on fitness over social than non-social paths in most species (Smith & Blumstein, 2007). Personality appears to be fundamentally social, perhaps reflecting the diversity of social and sexual strategies that can prosper in socially variegated groups that confront fluctuating, heterogeneous environments. This might be especially true for human personality after our species achieved 'ecological dominance' (i.e. reliable mastery of food acquisition and protection from predators and other hazards), which somewhat buffered our ancestors from spatiotemporal variation in the non-social environment (Alexander, 1989). Explicit arguments that negative frequency-dependent selection could maintain genetic variance in specific personality traits have been proposed by Gangestad & Simpson (1990) for female sociosexuality (i.e., promiscuity) and by Mealey (1995) for psychopathy.

Another application of negative frequency-dependent selection to explain personality has been proposed by Rushton (1985) and extended by Figueredo et al. (2005a, b). They argue that virtually all human individual differences, including broad personality factors, intelligence, attachment styles, reproductive strategies, growth, longevity, and fecundity, may reflect a single underlying 'life-history' dimension of variation in the organism's allocation of investment in growth vs. survival vs. reproduction across the life-course. Drawing a parallel to a similar, well-established dimension of between-species differences in evolutionary ecology, they suggest that this life-history dimension is maintained by negative frequency-dependent selection within and across human groups. A fortuitous side-effect is that such variation reduces within-group and between-group competition by allowing individuals and groups to fill different socio-environmental niches. Figueredo et al. (2005a, b) hypothesized that if a broad set of physical and psychology traits (e.g. intelligence, personality traits, sociosexuality, longevity) are subject to hierarchical factor analysis, a superordinate 'K-factor' will emerge that reflects variation on this life history dimension (note that this hypothesized K-factor is distinct from the *f*-factor discussed above).

A critical point from an evolutionary genetic perspective is that frequency-dependent selection (like any form of balancing selection) is only able to maintain polymorphisms at a few major loci (Turelli & Barton, 2004; Kopp & Hermisson, 2006). As a consequence, frequency-dependent selection on the K-factor would only be possible if a few polymorphisms would function as 'switches' that could simultaneously alter the development

and expression of all those many traits the K-factor aims to explain, including some of the most important emergent traits at the downstream end of the watershed model (Figure 1), such as longevity, growth, intelligence, and fecundity. As long as there is no evidence that these 'polymorphisms for almost everything' exist, future research on life history variation should distinguish more carefully between (1) mutation-selection balance for downstream traits like longevity, growth, intelligence, and fecundity, (2) the condition- and environment-dependent adjustment of reproductive strategies (Gangestad & Simpson, 2000; Penke & Denissen, 2007), and (3) balancing selection for various independent personality traits at a more upstream level of genetic complexity.

To summarize, balancing selection by environmental heterogeneity, often mediated by negative frequency-dependent selection, seems the most plausible mechanism for maintaining genetic variation in personality traits. In contrast, balancing selection is implausible for maintaining genetic variation in downstream fitness-related traits, such as intelligence.

The Role of the Environment in Evolutionary Genetics

Evolutionary adaptationism is often misunderstood as overemphasizing genetic influences and neglecting environmental influences on behaviour. In fact, the opposite is generally true: evolutionary theory is fundamentally environmentalistic (Crawford & Anderson, 1989), because it is about the adaptive fit of an organism to its environment – a GxE interaction.

Phenotypic plasticity. One form of this interaction – selection - has already been discussed. Selection acts only upon the complete phenotype, which is at the most downstream end of the watershed model (Figure 1), at the level of overall fitness. But GxE interactions take place all the way upstream, up to the molecular level, where transcribed genes can only produce specific proteins if the required amino acids are present (ultimately a nutritional issue). From this perspective, it is hardly surprising that identical genotypes can produce very distinct phenotypes. This phenomenon is called *phenotypic plasticity*, and it is probably ubiquitous in nature (West-Eberhard, 2003). The environment thus has two distinct roles in evolutionary genetics: It interacts with the genotype in the ontological development of the phenotype, and then, as a selective regime, determines the phenotype's fitness and decides its fate.

Ideally, organisms would fare best if they could fit themselves perfectly and instantly to the environmental demands in every situation – morphologically, physiologically and behaviourally. Of course, developmental constraints render such an unlimited degree of phenotypic plasticity implausible for physical traits (e.g., no drowning mammal can suddenly develop gills, no matter how advantageous such a transformation would be). In contrast,

unlimited *behavioural* plasticity has been an attractive scientific vision for a long time, both in psychology (i.e., radical behaviourism) and biology (i.e., traditional behavioural ecology; Krebs & Davies, 1997). But even in the case of behaviour, unlimited plasticity is impossible to achieve adaptively, because the environment does not reliably signal the likely fitness payoffs of all possible behavioural strategies (see Miller, in press). In a complex world, environmental cues that can guide adaptive behaviour are inherently noisy, often contradictory, and unpredictably variable (Brunswick, 1956; Gigerenzer, Todd & the ABC Research Group, 1999). The unreliability of environmental cues means that any behavioural plasticity based on trial-and-error learning must take time, because it must depend upon a decent sample of action-payoff pairings. Thus, given the complexities of real-world environments, organisms cannot instantly discern and implement the optimal behavioural strategy, so fitness-maximizing by unlimited behavioural plasticity is an impossible ideal.*Universal constraints on phenotypic plasticity.* Fortunately, evolution constrains behavioural plasticity in adaptive directions, just as it constrains physical development. As long as environmental features are sufficiently stable and fitness-relevant (e.g. women get pregnant but men don't, rotten food is toxic, children demand more care and protection than adults), natural selection will fixate psychological mechanisms such as emotions, preferences, and learning preparednesses that adaptively bias our reactions to the environment over ontogenetic development. This relieves us from the impossible task of learning our most basic behavioural dispositions *de novo* every generation (Tooby, Cosmides & Barrett, 2005; Barrett, 2006; Figueredo et al., 2006). These kinds of GxE interactions – interactions between inherited psychological adaptations and ancestral adaptive challenges - are the central subject of adaptationistic evolutionary psychology. Cervone (2000) argued that they also constitute interesting building blocks for personality theories. However, adaptationistic evolutionary psychology deals principally with interactions between the universal genetic make-up of our species and fitness-relevant aspects of the environment that reoccurred over evolutionary time. Such interactions might explain the non-genetic variation in some personality domains (e.g. attachment styles - Buss & Greiling, 1999), but are largely uninformative about heritable personality differences.

Individual constraints on phenotypic plasticity. When selection cannot deplete all genetic variation (for any of those reasons discussed above), different genotypes persist simultaneously in the population. Genotypes might differ in their response to the environment, leading to the statistical effect that behaviour geneticists refer to as a GxE interaction (Moffitt, Caspi & Rutter, 2006). In humans, such interactions have been found, for example, between the MAOA polymorphism and childhood maltreatment in the development of conduct behaviour (Caspi et al., 2002), and between the 5-HTT polymorphism and stressful life events in the development of depressiveness (Caspi et al., 2003). By

systematically varying both the genotypes and the environments, evolutionary geneticists studying non-human species can determine a typical response function for each individual genotype, a so-called *reaction norm* (Via et al., 1995) (see Figure 2). While a GxE interaction is a population statistic, an individual reaction norm can be regarded as a characteristic of an individual genotype (Pigliucci, 2005). Reaction norms were originally used to study the developmental plasticity of morphological or life-history traits, but when behavioural ecologists realized the systematic limits of behavioural flexibility, they began to view heritable response styles – known to psychologists as personality traits – as behavioural reaction norms. (Sih et al., 2004; van Oers et al., 2005).

Insert Figure 2 about here

While behavioural ecologists discovered animal personality only recently (Sih et al., 2004), their immediate equation of personality traits with individual reaction norms helped them to circumvent the 'person-situation debate' in personality psychology (Mischel, 2004). Instead of looking for personalities that reliably predict behaviour across all possible situations, or situations that reliably predict behaviour across all possible personalities, behavioural ecologists quickly adopted a reaction-norm view of personality that neatly resembles the *personality signatures* view of Mischel and Shoda (1995). Personality signatures describe stable patterns of contingent (if-then) relationships between personalities, situations, and behaviours – just as reaction norms describe stable contingencies between genotypes, environments, and phenotypic outcomes. These person-situation contingency profiles turn out to show reasonable consistency (Mischel & Shoda, 1995; Borkenau, Riemann, Spinath & Angleitner, 2006), but it is a different type of consistency than the well-known rank-order stabilities of personality traits across situations (Mischel, 2004). However, unlike individual reaction norms, personality signatures describe environment-behaviour functions for persons, not for genotypes. Although Mischel and Shoda (1995) acknowledge the possibility that genes influence personality signatures, their Cognitive-Affective Personality Systems model emphasises the importance of learned beliefs, appraisals, expectancies, and goals, organized in cognitive-affective units. However, personality signatures show substantial heritabilities (Borkenau et al., 2006), so these cognitive-affective units are apparently influenced by genetic variation, and a genotype-oriented reaction-norm view may be appropriate.

To describe an individual reaction norm does not require a mechanistic model of the psychological processes that mediate between environmental contingencies and behaviours. Reaction norms simply relate dimensional variations in genotypes and environments to variations in behavioural outcomes. Thus, the *shapes* of individual reaction norms are what can be equated with personality traits (van Oers et al., 2005). While reaction norm shapes can be simple (e.g. linear) when relating polymorphisms at a single gene locus to the

environment (as for example in Caspi et al., 2003), they can become more complex when polygenic genotypes (as in the case of personality traits) are related to the environment (de Jong, 1990). Furthermore, while the studies by Caspi et al. (2002, 2003) provide examples of reaction norms in personality development (i.e., GxE interactions during childhood predict adolescent personality), the concept of individual reaction norms is not limited to a developmental time frame. Reaction norms can also describe GxE interactions in the production of ongoing behaviour, analogous to Mischel and Shoda's (1995) personality signatures.

Note that reaction norms can be determined for any phenotypic trait, including cognitive abilities. However, we believe that reaction norms are much more informative for personality traits than for cognitive abilities. Reaction norms provide an elegant tool to disentangle the twofold role of the environment for personality traits as both a source of phenotypic plasticity within a generation and of fluctuating selection pressures across generations. This more nuanced view of environmental influences on behaviour is unnecessary for fitness components such as cognitive abilities that are more likely under mutation-selection balance, in which case selection pressures push traits in roughly the same direction (minimum genetic mutation load, maximum phenotypic efficiency) across all kinds of environments. In addition, the phenotypic plasticity of general intelligence apparently reflects simple condition-dependency, as *g* declines with adverse environmental influences (e.g. starvation, dehydration, sickness) that decrease general condition (see Miller & Penke, 2007). Since the genetic variation in *g* accounts for almost all genetic variation in cognitive abilities (Plomin & Spinath, 2004), the reaction-norm view seems less helpful for cognitive abilities than for personality traits.

Individual Reaction Norms and the Hierarchical Structure of Personality Traits

The hypothesized existence of complex individual reaction norms has an interesting implication for the hierarchical structure of personality traits. We illustrate this with an example modified from van Oers et al. (2005) (Figure 2): Let two personality traits (say, depressiveness and anxiousness) be described by reaction norms to a continuum of environmental stress. For depressiveness, we assume the simple reaction norm found by Caspi et al. (2003) (Figure 2a): Genotype A shows high depressiveness in highly stressful environments (i.e., point Z), medium depressiveness in the less stressful environment Y, and no depressiveness in the calm environment X. Genotype B shows the same reaction on a lower level (i.e., B's individual reaction norm has a smaller slope), while C is resilient in all environments. Let us now assume a hypothetical, more complex reaction norm for anxiousness based on the same three genotypes and environments (Figure 2b). In environment Z, the rank order of the anxious reactions is the same as for depressive

reactions for the three genotypes (A > B > C), implying a positive genetic correlation between the two traits in this environment. (Note that the reaction norm model assumes that all relevant environmental influences are captured either in the environmental dimension or in confidence intervals around the reaction norm functions, so that we can speak of genetic correlations here.) The critical effect of complex reaction norms is revealed at the other two points of the environmental dimension: In environment Y, genotypes A and C react with an identical degree of anxiety, and genotype B reacts only slightly more strongly. The genetic correlation between anxiety and depressiveness in this environment would therefore be close to zero. Finally, in environment X, the rank order of the anxious reactions for the three genotypes is the inverse of their rank order for depressive reactions in the same environment, leading to an apparent negative genetic correlation. In this purely hypothetical example, subsuming both traits in a higher order factor (here neuroticism) would not be warranted, since their relationship is highly context-dependent. More generally, delineating hierarchical personality structures would be impeded by sign changes in the genetic correlations among personality traits measured across environments. Therefore, van Oers et al. (2005) regard the absence of sign changes in genetic correlations of related facet traits across environments as a necessary condition for the existence of superordinate personality domains. This leads us to specific requirements concerning how personality-related genes must affect multiple personality traits

Structural pleiotropy. Except for some rare and evolutionarily unstable cases (called linkage disequilibria), genetic correlations are always caused by pleiotropy, the effect of polymorphisms on multiple traits (Roff, 1997). Pleiotropy has been shown for the hierarchical structure of the FFM in twin studies (Yamagata et al., 2006; Jang et al., 1998, 2002; McCrae et al., 2001). But as in our hypothetical example, pleiotropy in itself does not prevent sign changes in genetic correlations between traits across environments. Sign changes can only be prevented by functional, physiological, or developmental links between the effects of polymorphisms on one trait and their effects on another trait. Such a condition, called *structural pleiotropy*, poses a developmental constraint on the independent phenotypic expression of both traits in all environments (de Jong, 1990). To be sure, structural pleiotropy does not mean that complex reaction norms, such as those depicted in Figure 2b, are theoretically implausible. Instead, the central point is that, for two traits to be facets of the same higher-order factor, the rank order of the phenotypic effects produced by different genotypes must not reverse across environments. The traits in Figures 2a and 2b cannot belong to the same higher-order factors, but both can, together with other traits, belong to different factors.

An implication of structural pleiotropy is the existence of underlying neurogenetic *mechanisms* (e.g. neurotransmitter or endocrinological systems) that are shared by all facets

of a higher-order trait. An advantage of viewing personality traits as individual reaction norms is that these mechanisms, which should be closely linked to the genotype, can be explicitly separated from the environmental factors with which they interact. In this way, individual reaction norms come much closer to the original personality trait definition by Allport (1937) as "psychophysical systems that determine [an individual's] unique adjustment to his environments" (p. 48), than to the purely descriptive, empirically derived factors that are normally posited in personality psychology, and they also avoid the often-criticized circularity of the definition of traits as aggregated instances of behaviour, which are then used to predict…behaviour (see Denissen & Penke, 2006).

A developmental perspective. If broad personality domains exist because of shared underlying mechanisms (i.e., because structural pleiotropy preserves the sign of genetic correlations between traits across environments), then personality structure likely develops top-down, from these mechanisms to higher-order personality domains (e.g. neuroticism) to lower-order personality facets (e.g. anxiousness, depressiveness). Over the lifespan, these mechanisms might modulate the cognitive and affective experiences that individuals acquire through interacting with their environments. Thereby, they might act as forms of 'prepared learning' (Figueredo et al., 2006) for the acquisition of the cognitive-affective units emphasized by Mischel and Shoda (1995), and as 'experience-producing drives' (Bouchard et al., 1996) that motivate active niche selection (Denissen & Penke, 2006). These shared mechanisms would be the ties that bind different facet traits within broader personality domains. Together with the influence of unique genetic variation on the level of lower-order traits (Jang et al., 1998, 2002), this would result in the hierarchical structure of personality traits, down to the level of idiosyncratic habits and behavioural patterns.

The dimensionality of personality. Note that this theoretical argument makes no commitment to any particular number of highest-order mechanisms or their interactions. The prominence of the FFM led evolutionary psychologists (MacDonald, 1995, 1998; Nettle, 2006a), including us (Denissen & Penke, 2006), to hypothesize selection regimes at this hierarchical level. However, some of the FFM dimensions may still share some common mechanisms that render them not entirely orthogonal (Jang et al., 2006). For example, Jang et al. (2001) showed a significant amount of genetic overlap between the domains of neuroticism and agreeableness, which was partly explained by the 5-HTTLPR polymorphism. It is also possible that several neurogenetic mechanisms interact to form what we observe as broad personality dimensions. Jang et al. (2002) showed that two independent source of genetic variance were necessary to explain the variation of each of the FFM personality domains. If these independent genetic sources reflect independent neurodevelopmental mechanisms, environments may exist in which they no longer contribute to the same behavioural dispositions (de Jong, 1990), and are no longer under parallel selection

pressures (e.g., see Figure 2b). The bottom line is that the genetic architecture of personality might not reflect the phenotypic structure of established factor-analytic models, though it would be surprising if it was completely different. At any rate, we believe that the reaction norms of structurally independent mechanisms constitute a promising level of analysis for an evolutionary personality psychology.

Operationalising Individual Reaction Norms

The natural approach to the study of reaction norms would be to observe the behavioural reactions of different genotypes along a well-quantified environmental continuum. However, the standard methods used by evolutionary geneticists to study non-human species (e.g. inbred strains) are of course not available to human psychologists. Identical twins provide a surrogate (Crawford & Anderson, 1989), though a limited one, since only two copies of each genotype exist and the environment cannot be varied experimentally. One alternative is to relate single polymorphisms to behavioural variations that are contingent on certain environmental variables (as done by Caspi et al., 2002, 2003, see also Moffitt et al., 2006). While this approach will certainly become common in the near future as a consequence of cheaper, faster, and more powerful genotyping methods (e.g. DNA microarrays), such studies might still fail to capture the complex polygenic nature of personality traits in the near future.

Another alternative is to assess individual differences directly at the level of hypothetical underlying mechanisms. Here, an *endophenotype* approach appears highly promising. Endophenotypes are phenotypic structures and processes (e.g. neurotransmitter systems or hormone cascades) that can be quantified directly (e.g. by neuroimaging or blood sampling) and that mediate between genes and more complex or abstract traits (Boomsma, Anokhin & DeGeus, 1997; Cannon & Keller, 2005). In the watershed model (Figure 1), currently measurable endophenotypes tend to be located at a very upstream level. In the exemplary case of neuroticism, amygdala reactivity (Hariri et al., 2002, 2005) provides an especially good example of a mediating endophenotype, though there are likely several others. Sih et al. (2004), for example, highlighted the role of hormonal mechanisms in animal personality.

Of course, all of these approaches are much harder work than using classical personality questionnaires, so they will probably remain a minority interest within personality psychology. But even questionnaires can be improved to reflect a view of traits as individual reaction norms, by explicitly assessing behavioural reactions to specific fitness-relevant situations, instead of aggregating across arbitrary modern environments (Mischel & Shoda, 1995; Denissen & Penke, 2006). For example, some people may be socially confident at informal parties but not at public speaking, whereas for others, the opposite may apply. To

class them both as 'extraverts' may conflate disparate genotypes that lead to distinct endophenotypes, behavioural strategies, reaction norms, and fitness payoffs. Indeed, the quest to maximize internal consistencies within personality scales (e.g. by homogenizing the environmental circumstances of behaviours) may lead personality psychologists to eliminate some of the questionnaire items that are most informative about GxE interactions and individual reaction norms.

An Evolutionary Genetic Model of Personality

The evolutionary genetics of personality can be summarized in the model depicted in Figure 3.

Insert Figure 3 about here

For natural selection, the structure of individual differences is fairly straightforward and simple: all living organisms vary on one major dimension - fitness – which is their statistical propensity to pass their genes on to future generations to come. Miller's (2000c) *f*-factor represents this dimension at the very top of any evolutionary hierarchy of heritable differences – or at the very downstream end of the watershed model (which is why we put *f* at the bottom in Figure 3). The upstream-downstream dimension is shown on the left. Since virtually all psychological differences studied so far show heritability, the central question for evolutionary personality psychology is: how do psychological differences relate to the *f*-factor?

All heritable psychological differences begin with a set of genes that influence the functioning of neurophysiological mechanisms (detectable as endophenotypes). A simplification of the model is that environmental influences are omitted at the genetic and endophenotype levels. This seems justifiable, since environmental effects are probably smaller (due to developmental canalization) at the upstream levels than at the downstream levels. One or several of the mechanisms on the endophenotype level result in the behavioural tendencies that we observe as traits and abilities at the dispositional level. In relevant situations, these dispositions influence behaviour, and from this point onward, they affect the biological fate of the organism: behaviour influences the organism's adaptive fit to the current environment, and thus influences its overall reproductive success.

Genetic variation in personality differences might be maintained by selective neutrality, mutation-selection balance, or balancing selection – each of which would leave distinctive footprints in a trait's genetic architecture. We have argued that selective neutrality is implausible for most personality differences, given their pervasive effects on fitness-relevant life outcomes. Mutation-selection balance requires that (1) a trait is influenced by enough genes that new mutations disrupt its efficiency at a steady rate, and (2) selection favours trait efficiency strongly enough to eliminate these mutations after some evolutionary

time. As a consequence, these traits will be influenced by many interdependent neurogenetic mechanisms on the endophenotypic level, and will show substantial additive genetic variation that affects trait efficiency and thereby influences fitness. Environmental influences on such traits will be mediated mostly by their effects on the organism's overall condition. In line with Miller (2000c; Prokosch et al., 2005), we propose that general intelligence belongs to this category of traits under mutation-selection balance. In this case, the upstream ability mechanisms I and II in Figure 3 could be, for example, the efficiency of cerebral glucose metabolism and the accuracy of prefrontal programmed cell death during adolescence, and the downstream ability mechanisms III and IV could be processing speed and working memory capacity (see Jensen, 1998).

An evolutionary genetic conceptualisation of cognitive abilities would thus be: individual differences in the functional integrity of broad systems of the adaptive cognitive apparatus, caused by an individual's load of rare, mildly harmful mutations. In short, cognitive abilities are cognitive fitness components. For such traits, a low mutation load is always beneficial, regardless of the environment.

By contrast, the phenotypic and genetic characteristics that are typically found in studies of personality traits (like those in the FFM) suggest that balancing selection is maintaining the genetic variance in most (if not all) personality traits. Balancing selection can favour different traits in different social or non-social environments. In addition to this role as a varying selection pressure on personality traits, the environment serves a second role earlier on, when interacting with the neurophysiological architecture of the trait (i.e., its personality mechanism or mechanisms) through a reaction norm to form a behavioural tendency. This twofold role may make the environmental influences on personality traits under balancing selection much more numerous, complex, and differentiated than those affecting traits under mutation-selection balance (which may reflect general phenotypic condition rather than specific environmental contingencies). On the other hand, the upstream genes and endophenotypes of personality traits under balancing selection will be fewer than those of cognitive abilities under mutation-selection balance.

An evolutionary genetic conceptualisation of personality traits would thus be: individual differences in genetic constraints on behavioural plasticity, which lead to behavioural tendencies that follow individual reaction norms, and produce different fitness consequences in different environments. In short, personality traits are individual reaction norms with environment-contingent fitness consequences.

Where Do Common Psychopathologies Fit Into the Model?

While this review focuses on personality differences in the normal range, we would like to add some remarks on the place of polygenic psychopathologies in our model. In an

extensive discussion of the evolutionary genetics of common psychopathologies, Keller and Miller (2006a, b) argued that mental disorders such as schizophrenia and bipolar disorder are best conceptualized as traits under mutation-selection balance. Indeed, they cite evidence that these disorders possess all the expected characteristics (Table 1). In our model, these disorders are thus fitness components that mark the low end of the *f*-factor. Some common psychopathologies, however, show clear relationships to personality traits in the normal range, especially to high neuroticism and low agreeableness (Saulsman & Page, 2004). These disorders might be viewed as maladaptive extremes of normal personality traits - rare genotypes that will sometimes occur in polygenic traits due to sexual recombination. For example, extreme extraversion (e.g. impulsive, narcissistic, histrionic, and/or promiscuous behaviour) and extreme introversion (e.g. schizoid, avoidant, hermit-like withdrawal from all social contact) may both be too extreme to yield fitness benefits in any plausible niche (MacDonald, 1995, 1998). But extreme values on normal traits alone are usually insufficient for the occurrence of psychopathologies (Saulsman & Page, 2004), and even high neuroticism and low agreeableness can be adaptive (though not necessarily socially desirable) when the social environment is harsh, risky, and unforgiving, or when it is exploitable and gullible, respectively (Nettle, 2006a; Denissen & Penke, 2006).

An alternative is that modern societies produce mismatches between heritable temperaments and available niches. For example, Harpending and Cochran (2002) argue that the very same 7R-DRD4 allele that predisposes children to attention deficit hyperactivity disorder (ADHD) today may have been adaptive if these individuals lived in a violently competitive, polygamous society. More generally, genetic variation maintained by environmental heterogeneity implies that there are always some individuals for whom an optimal niche does not currently exist. Similarly, negative frequency-dependent selection implies that there are cases in which an individual's usual niche is overcrowded and competitive.

In addition, the pathological nature of personality disorders might also result from a high mutation load, but receive their characteristic symptoms from an interaction of this load with certain personality traits. For example, very high openness to experience might overwhelm individuals whose cognitive abilities are compromised by a high mutation load and consequently lead to a diagnosed schizotypic personality disorder, while it might appear attractive in less mutation-laden individuals, who are able to turn it into exceptional creative outputs (see Nettle, 2006b; Nettle & Clegg, 2006; Keller & Miller, 2006b).

Practical Implications for Behaviour Genetics

An evolutionary genetic framework for personality psychology has some practical implications for behaviour genetic studies:

1. Demonstrating that a personality trait is heritable had become scientifically unsurprising by the early 1990s (Turkheimer & Gottesman, 1991), and is not very informative about a trait's nature or etiology, since it confounds information about a trait's evolutionary history, structure, and GxE interactions (Stirling et al., 2002). This is especially true for the broad-sense heritabilities that are estimated in the classical twin design, since they do not distinguish between V_A and V_{NA} (Keller & Coventry, 2005), which is very important in evolutionary genetics (Merliä & Sheldon, 1999). We therefore concur with Keller and Coventry (2005) that more studies using the extended twin-family design (Neale & Maes, 2004), or other designs that unconfound V_A and V_{NA}, are highly desirable, especially when testing evolutionary genetic hypotheses (cp. Table 1).
2. Because of the great datasets and twin registries already available, classical twin studies will probably remain the most common type of behaviour genetic publications. However, such studies would be more informative (or less misleading) about the evolutionary genetics of traits if their underlying statistical assumptions were made more explicit. Many personality psychologists seem not to appreciate that classical twin studies can yield a wide range of mathematically equivalent parameter estimates (e.g. for additive genetic vs. dominance vs. epistatic effects) that have very different implications for the evolutionary histories of the traits under investigation (Keller & Coventry, 2005; Coventry & Keller, 2005). We therefore suggest that future publications of classical twin study results make use of the technique developed by Keller and Coventry (2005) and fully disclose the confidence intervals and parameter spaces for their results.
3. The equation of personality differences with individual reaction norms highlights the fact that GxE interactions are ubiquitous in nature. Similarly, balancing selection on personality traits due to spatiotemporal heterogeneity of selection pressures suggests that GxE correlations are fairly common. Unfortunately, the usual approach in quantitative behaviour genetic studies is additive variance decomposition, which hides both GxE interactions and GxE correlations in apparent main effects (Purcell, 2002). However, the necessary statistical modelling techniques exist to identify such interaction effects (Neale & Cardon, 1992; Purcell, 2002), and evolutionary genetics suggests that they should be used more frequently.
4. For the same reason, the use of personality trait measures (especially self-report questionnaires) that aggregate across situations might have reached its limits in clarifying the genetic architecture of personality (Ebstein, 2006). Both endophenotype approaches and phenotypic measures that aim to keep person and situation separated (Dennisen & Penke, 2006; Mischel & Shoda, 1995) provide better alternatives.
5. Calculating the coefficient of additive genetic variance (CV_A) of a trait, which is very informative about its evolutionary history (Houle, 1992; Stirling et al., 2002), requires a ratio-scale measure (i.e., a measure with a meaningful zero point). Personality questionnaires with rating scales fail to reach this standard. It would be very helpful if valid, ratio-scaled personality measures (e.g. based on quantitative endophenotypes or behaviours measured with regard to their energy output, temporal duration, or act frequency – see Buss & Craik, 1983) could be developed and used in quantitative behaviour genetic studies.

6. We predict that 'gene hunting' studies will continue to be more successful in revealing the molecular genetic architecture of temperamental personality traits than of general cognitive abilities or polygenic mental disorders (Ebstein, 2006; Plomin et al., 2006; Keller & Miller, 2006a). Evolutionary genetic theory gives a straightforward reason why: while personality traits will be influenced by a limited set of high-prevalence alleles (plus maybe several rare ones, see Kopp & Hermisson, 2006), general intelligence and psychopathologies like schizophrenia will be influenced by rare, recessive, mildly harmful mutations that vary between samples, since they are equally likely to occur at thousands of different, otherwise monomorphic loci, and are removed fairly quickly by selection once they arise. (Note that this goes beyond Kovas and Plomin's (2006) concept of 'generalist genes', which proposes that the *same* large set of weak-effect polymorphisms underlies cognitive functioning in every individual.) While we do not argue that molecular behavioural geneticists should refrain from studying *g*, common psychopathologies, and other fitness components, we suggest that they take evolutionary genetic predictions of the likely genetic architecture into account when planning studies and interpreting results. A simple first step would be to call the underlying polymorphisms what the empirical evidence suggests they are – rare mutations.
7. More generally, evolutionary genetics provides a rich theoretical source of hypotheses that should inspire and guide future behaviour genetic studies. For example, factor V (openness to experiences/intellect) is the only domain of the FFM that shows reliable correlations with general intelligence (e.g. DeYoung et al., 2005). From an evolutionary genetics viewpoint, this puts factor V in an ambiguous position: does it reflect an ESS under balancing selection (see Denissen & Penke, 2006; Nettle, 2006a), or an important component of the *f*-factor, which should be under mutation-selection balance? If factor V is under balancing selection, its molecular genetic basis should be much easier to identify – especially if behaviour genetics researchers statistically control for general intelligence when investigating polymorphisms that may influence factor V. Other exemplary evolutionary genetic hypotheses can be found in Miller (2000c) and Keller (in press).

Conclusion

Evolutionary psychology has made so much progress in the last 15 years by relying on an evolutionary adaptationist metatheory that guides the identification of ancestral adaptive problems, the likely psychological adaptations that they favoured, and the likely design features of those adaptations that can be investigated empirically (Andrews et al., 2002; Buss, 1995). We have argued that evolutionary genetics can provide a similarly powerful approach to the study of heritable individual differences in personality.

Evolutionary genetics is itself a fast evolving field. While we tried to give an up-to-date overview of evolutionary genetic principles that seemed most relevant for personality psychology, some of those principles will probably be refined, extended, or challenged in the near future. They should thus be viewed as the provisional, current state of the art, not as biological commandments carved in stone. Still, they may help personality psychology enormously by clarifying what is evolutionarily possible and plausible, and what is not. This

way, evolutionary genetics can provide personality psychology with new hypotheses, guidance on how to interpret results, and constraints on theory formulation. Ultimately, our grandest hope for evolutionary personality psychology is that, given the enormously rich phenotypic and behaviour genetic datasets on human personality, it might identify new evolutionary genetic principles that also apply to other kinds of traits and other species.

We reviewed the current answers that evolutionary genetics can give to a question that has rarely been asked in psychology: how is the genetic variation that obviously underlies most human differences, including personality differences, maintained in the population? It turned out that only two answers are sufficiently plausible for personality differences: either (1) the trait is dependent on so many genes that a balance between rare, mildly harmful mutations and counteracting selection occurs, or (2) variation in the structure of the physical or social environment leads to spatiotemporally fluctuating selection for different alleles. Both evolutionary genetic mechanisms will lead their affected traits to have certain distinctive characteristics and underlying genetic architectures. We concluded that the first process (mutation-selection balance) probably maintains genetic variance in cognitive abilities, while the second process (balancing selection by environmental heterogeneity) probably maintains genetic variance in most personality traits. Thus, cognitive abilities are best conceptualised as cognitive fitness components, while personality traits reflect individual reaction norms with environment-contingent fitness consequences.

Important tasks for future studies include delineating the hierarchical structure of fitness components (with the *f*–factor on the top) and identifying the exact fitness-related costs and benefits associated with each personality trait, as well as the environmental niches that structure those costs and benefits. Social niches with different degrees and forms of competition are especially good candidates for the latter. A promising road for process-oriented personality psychologists is studying the psychological mechanisms that lead to active niche selection, including adaptive self-assessments (Tooby & Cosmides, 1990; Penke & Denissen, 2007; Penke et al., in press) and experience-producing drives (Bouchard et al., 1996).

Finally, we wish to reemphasise that most heritable individual differences are *not* adaptations in their own right. They reflect dimensions in the functional design of a species that tolerate some degree of genetic variation. Mutations at too many non-neutral loci will lead to a breakdown of adaptive design. Likewise, traits under balancing selection will tolerate polymorphisms only at a few specific loci, while all others loci (which affect the universal adaptative design of the trait) will be protected from large genetic variation by stabilizing selection. Adaptive individual differences exist, but only as conditional strategies that are implemented in universal (i.e. zero-heritability) adaptations and evoked by specific environmental cues (Tooby & Cosmides, 1990; Buss, 1991; Buss & Greiling, 1999). An

evolutionary personality psychology based on evolutionary genetics does not contradict this view. Instead, it complements evolutionary psychology by explaining what happens when genetic variation is introduced into systems of interacting adaptations (Gangestad & Yeo, 1997; Miller, 2000a). Since genetic variation is ubiquitous in personality psychology, evolutionary genetics is essential for an evolutionary personality psychology.

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Table 1:

A comparison of evolutionary genetic mechanisms for the maintenance of genetic variation and empirical predictions for affected traits

	Selective neutrality	**Mutation-selection balance**	**Balancing selection**
Genetic variation is due to…	…mutations that are not affected by selection because their phenotypic effect is unrelated to fitness in any environment.	…an accumulation of many old and new, mildly harmful mutations that selection has not yet wiped out of the population.	…polymorphisms that are maintained by selection because the fitness pay-off of their phenotypic effects varies across environments.
Predictions for an affected trait:			
Number of genetic loci (mutational target size)	(no prediction)	very large	medium
Number of polymorphic loci (QTLs)	likely small	large	small
Average gene effect on trait	(no prediction)	small	medium
Prevalence of polymorphisms	intermediate	rare	mostly intermediate
Relation to fitness	neutral	unidirectional	contingent on environment
Average fitness across environments	equal	unequal	approximately equal
Additive genetic variance (V_A)	(no prediction)	large	medium
Ratio non-additive to total genetic variance (D_α)	small	medium	high
Environmental variance (V_E)	(no prediction)	large	medium
Expression dependent on overall condition	no	yes	no
Inbreeding depression / heterosis effects	weak or none	strong	weak
Average social evaluation / sexual attractiveness	neutral	strong unidirectional favouritism	weaker, conditional favouritism

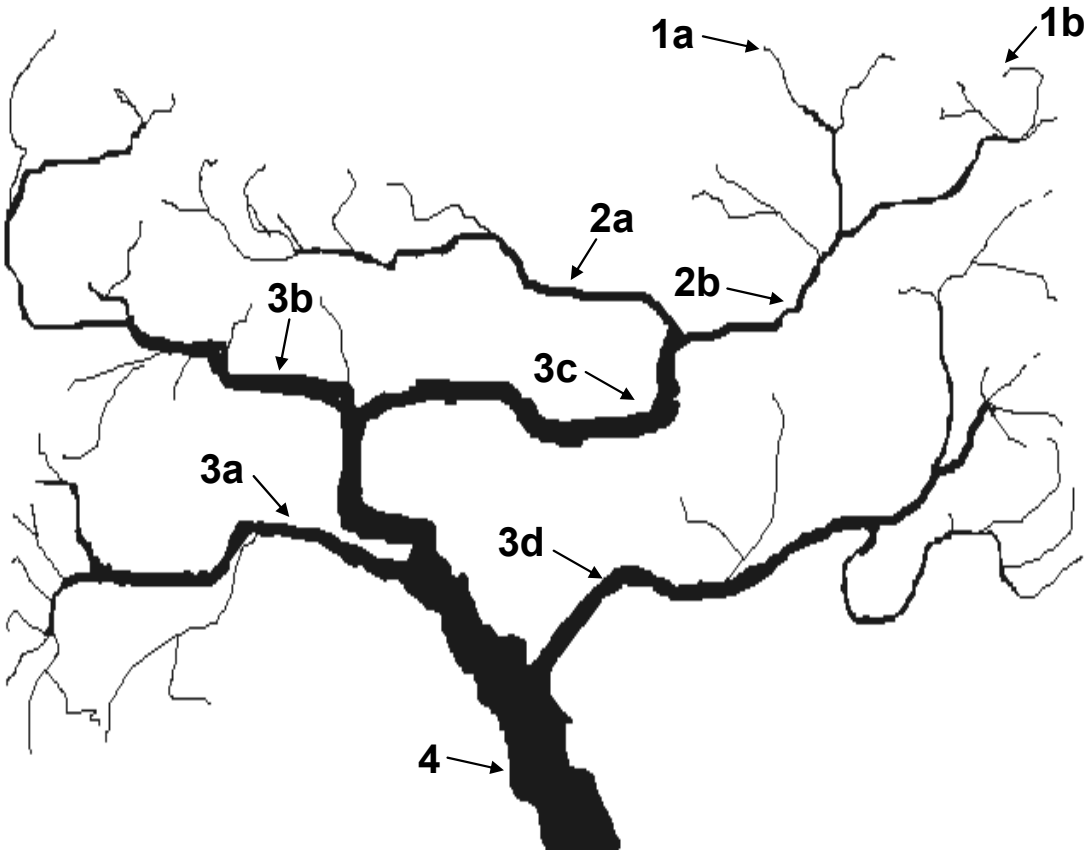

Figure 1: The watershed model of genetic variation

Mutations at specific loci (1a, 1b) disrupt narrowly defined mechanisms such as dopaminergic regulation in the prefrontal cortex (2b). This and other narrowly defined mechanisms contribute noise to more broadly defined mechanisms, such as working memory (3c). Working memory in conjunction with several other mechanisms (3a, 3b, 3d) affect phenotypically observable phenotypes, such as cognitive ability (4). If enough noise is present in the upstream processes, specific behavioural distortions may arise, such as mild mental retardation. All tributaries eventually flow into fitness. (Reproduced from Cannon & Keller, 2005, with permission from www.annualreviews.org.)

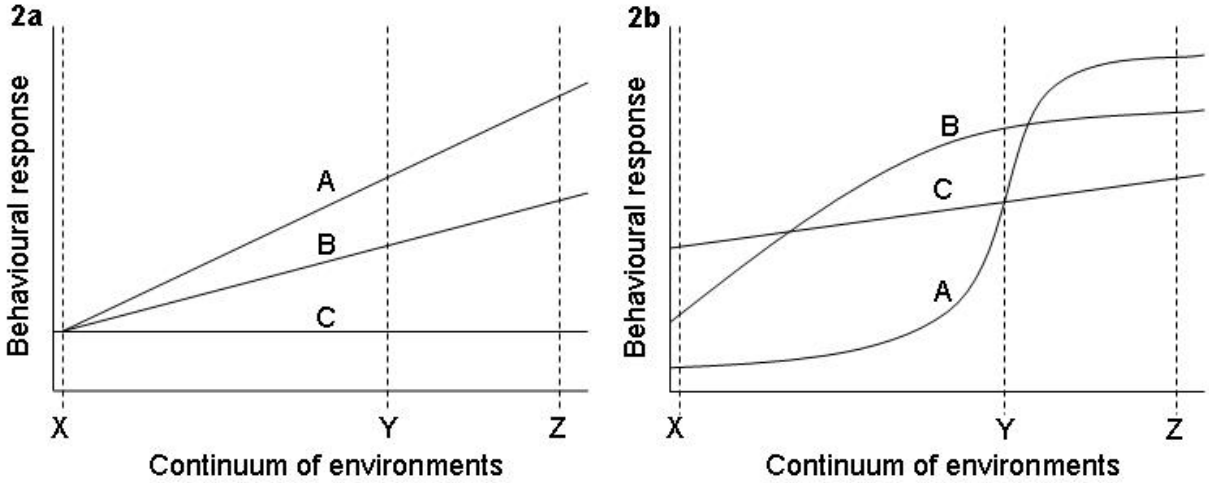

Figure 2: Two examples for individual reaction norms

Both figures show the individual reaction norms of three genotypes (A-C) along a continuous environmental dimension. The trait in Figure 2a has simple reaction norms, where all genotypes react linearly to environmental changes and differ only in their slope. The trait in Figure 2b has complex reaction norms, where genotype C reacts linearly and genotypes A and B react non-linearly in different ways. This leads to different rank orders of reaction strength at point X, Y, and Z on the environmental dimension, implying the absence of structural pleiotropy. (Figure 2b is redrawn after van Oers et al., 2005.)

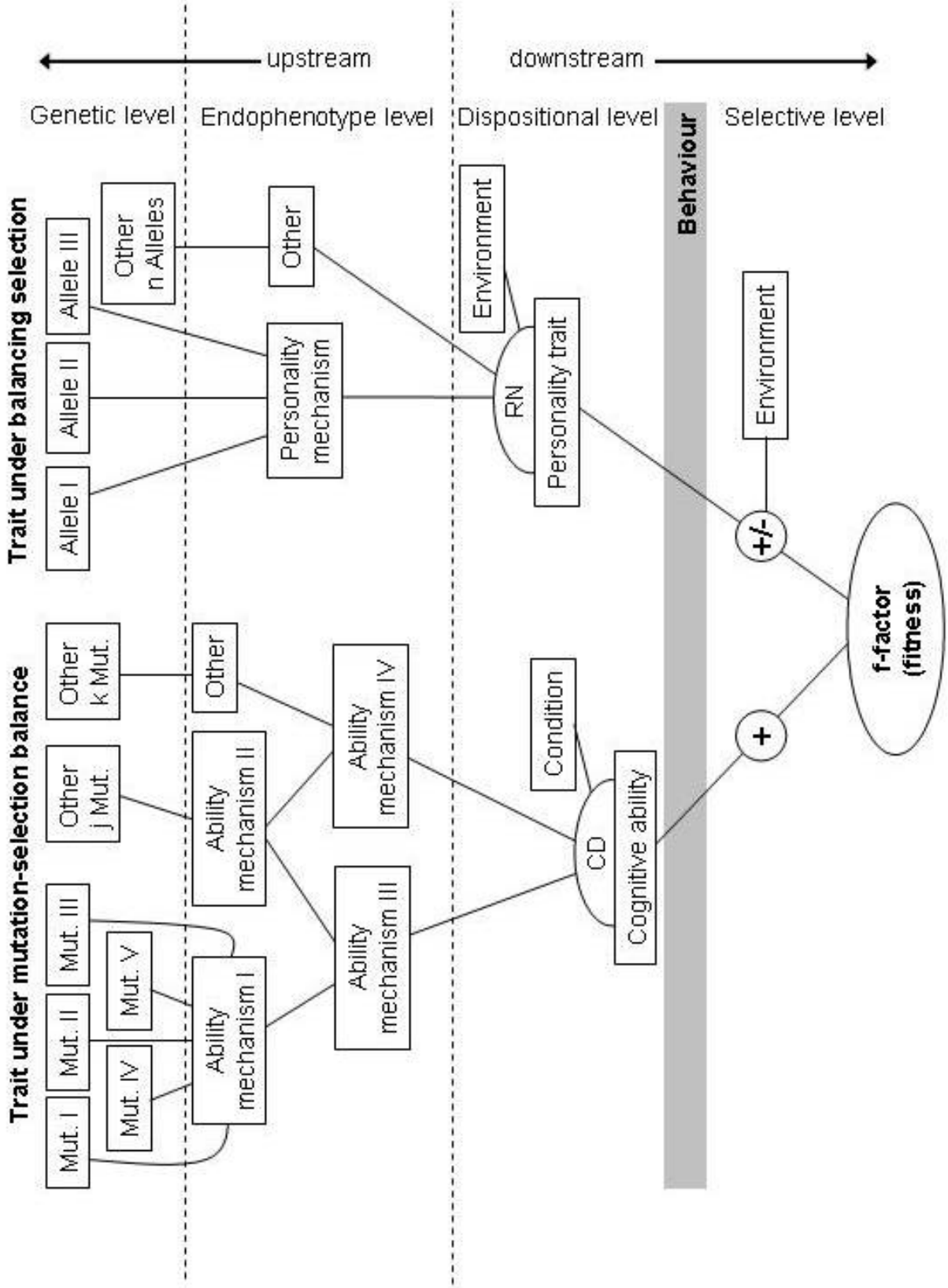

Figure 3: An integrative model of the evolutionary genetics of personality

Note: Mut.: mutation, CD: condition-dependency, RN: reaction norm

Open Peer Commentary

Out of the Armchair

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Abstract

Penke et al. (this issue) attempt to explain personality and cognition from theory rather than empirical study. This overstates the constraints on evolution, while underestimating the power of cross-species HapMap data to directly identify our evolutionary history. Independent of armchair-speculation, information benefiting human understanding, health, and well-being is flowing from exactly the research the target suggests should not be pursued.

The target begins, as does much of evolutionary psychology, from an assumption that human evolution is "finished": that we are in an evolutionary steady-state, with directional selection and its associated linkage-disequilibrium and departures from Hardy-Weinberg equilibrium long since washed away. This leads directly to models of residual heritability for ability as an irreducible legacy of IQ being distributed across thousands of mutable genes, and personality as a simpler system with variation retained due to correlations between genotype and survival being variable to the point of reversing in sign. This commentary focuses on the ability model and conclusions for research.

The target article ignores evidence from the HapMap (Wang, Kodama, Baldi, & Moyzis, 2006) and from candidate genes (Evans, Mekel-Bobrov, Vallender, Hudson, & Lahn, 2006) suggesting that much of human evolution has a recent history, not just over the last 500,000 years when brain size doubled, but including the period since some humans left Africa, and importantly, the 5-10,000 years since the invention of agriculture. These data showing recent and even current selection affecting neuronal function, as well as reproductive and immune function, protein and DNA metabolism, and cell-cycle control violate the assumptions on which the target article is based.

Despite there having been only one small genome-wide linkage scan for cognition, one pooled association study (with density an order of magnitude lower than believed adequate), and exactly zero dense genome-wide association studies for cognition, the

authors conclude that searching for genes for cognition is futile: too many to find, too small to be of use, and too variable to be easily marked. I suggest that, such data as are available support conclusions exactly opposite to those proposed.

The search for genes is already reaping rewards. The sole linkage scan report found three regions related to IQ (Posthuma et al., 2005), the pooled association study 6 regions (Butcher et al., 2005) (now replicated), and OMIM contains over 1000 major-effect genes for cognition helping elucidate pathways to normal ability. Multiple polymorphism-combinations suggest substantial normal single-gene effects on ability (Dick et al., 2007). Paradoxically, for the personality model of the target article, the success of cognition research great exceeds that of the search for personality genes (Willis-Owen & Flint, 2007).

The target makes many additional far-ranging claims about human evolution. They note that cognitive differences may be almost identical to total mutation load. However, while the phenotypic correlation between ability and developmental stability is robust, the sole (as yet unpublished) study on the genetic correlation between developmental stability and IQ found a genetic correlation of 0! Theory predicts it should be close to 1.0, and this represents a massive challenge to the genomic fitness-IQ model, suggesting that the FA-IQ correlation may be environmentally mediated.

Even if we accepted that variance in cognition reflects an inability to remove mutation, much else is left unexplained: for instance, why is mean IQ not much lower or much higher, despite exemplar groups differing by 1 or even 2 *SD* on mean IQ? This is empirical proof that far from being bound by an upper limit imposed by mutation, evolution can move human IQ over massive ranges. Tangentially, this raises the use of Houle's effect-size measure (∂^2/mean). This standardization was designed to highlight additive variance overshadowed by environmental and non-additive noise. In the case of intelligence, additive phenotypic effect-sizes are already clear, but it is also unclear that linear division by mean trait value is appropriate for ability. Ratio-scaled indices of cognition such as brain mass scale with body mass: should this not be first subtracted out? And frontal-lobes scale as a power function, invalidating linear transforms such as division.

The authors emphasize the *possible* reliance of cognition on many thousands of gene effects. However gene count *per se* is largely irrelevant for selection. Mutation is important in edge case such as traits outwith selective pressure, where we will expect equal accumulate rates for synonymous and non-synonymous mutations, and traits like human aging where the phenotype appears at too great a distance from reproduction to be selected on. However even if intelligence is distributed across the entire genome, its heritability leaves it highly modifiable, as the coefficient of selection remains dependent on selective pressure and selectability (i.e., heritability). Indeed, Stoltenberg (1997) suggested

replacing h^2 with “selectability” to highlight its meaning. It is worth noting too that the proposed pleiotropy of cognition with health and physical-fitness (Rae, Digney, McEwan, & Bates, 2003) simply enhances selection for cognition by selecting for higher IQ whenever strength or health has a positive effect on survival. This might even explain the paradoxical "excess" of human intelligence, despite strong reproductive selection against ability over the last century.

Finally the claim that small average-effects of single genes will hinder gene discovery is false. Rare alleles with major effects in these genes are excellent candidates for pedigree-based analysis and already researchers have discovered some 1000 brain function loci in this way (see OMIM). Similarly, the number of genes currently determining expression of a cognition does not limit the size of increases effected by single gene-changes. Indeed, the massive increase in human brain size over the last 500,000 years is probably due to just a handful of genes such as ASPM and MCPH1 (Zhang, 2003). Some of these show selection even in the last 5,000 years (Evans, Vallender, & Lahn, 2006), perhaps related to cognitive functions such as reading ability, language impairment, and / or social function, each of which is highly variable and heritable and every bit as dependent on the basic cellular material of the brain as is general ability. But each has shown highly significant linkage and association: Dyslexia appears to be controlled by a dozen or so genes (Bates et al., 2007), which are rapidly being understood at the level of neuronal development (Luciano, Lind, Wright, Martin, & Bates, in press). Human cognitive-genetics seems redolent with linkage disequilibrium signals associated with recent evolution, as is most of the human genome.

In summary, to understand how, when, and why cognition evolved requires hard empirical work detecting signals of selection, tracking genes over time, and establishing biochemical pathways… evolutionary theory *per se* is of limited utility.

Personality: Does Selection See It?

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Abstract

Selective neutrality offers a parsimonious explanation for personality variation. Bodily variations which do not compromise function (e.g. differences in intestine route) require no special explanation. Variations of the mind are not in principal different from those of the

body. A plausible explanation for such neutrality exists which does not require speculative stories about the circumstances of balancing selection.

Occam's razor has been loosely translated as "All things being equal, the simplest solution tends to be the best one." Principally for this reason, I have more sympathy than the authors with the selective neutrality of personality. As they observe, the precise route taken by the intestines may vary widely between people. This is an appealing example of neutrality because of the invisibility of intestines and their irrelevance to our social world. Personality traits seem different. We are struck on a daily basis by the differences between people. They form such a central part of social discrimination in our brief lifetimes that it is intuitively hard to accept that this wondrous human variety may be of no special evolutionary relevance. But would any biologist seriously consider devoting years to the study of individual differences in intestine route?

Personality differences may be no more than 'spandrels' of selection for pathogen resistance (Tooby, 1982). The evolutionary advantage of sexual reproduction is that genetic recombination gives us an edge in the human-pathogen arms race (Hamilton, Axelrod, & Tanese, 1990). The uniqueness of each individual—with respect to those polymorphisms that have no impact on the overall functioning of the organism---offers a moving target to fast-reproducing pathogens. "Pathogens select for protein diversity introducing the maximum tolerable quantitative variation and noise into the human system….protein variation gives rise to a wealth of quantitative variation in nearly ever manifest feature of the psyche; Tastes, reflexes, perceptual abilities, talents, deficits, thresholds of activation…" (Tooby & Cosmides, 1990, p.49). But such variation will not survive if it compromises the integratative functioning of the component parts and so threatens the complex evolved monomorphic design. In short, sustained variability points strongly to functional irrelevance. And if pathogens can explain the evolution of sexual reproduction in terms of the creation of genetic diversity, why should that diversity not be expressed as much through the mind (personality) as the body (intestines)? Biology does not respect any dividing line between them. Penke et al.'s scepticism about neutrality rests on 'strong evidence that personality differences have direct effects upon fitness'. Yet the most striking aspect of Figueredo, Sefcek, Vasquez, Brumbach, King, and Jacobs's (2005) review is the absence of unanimity about relationships between personality and fitness. For example, 'cheerful' adults have fewer health problems but cheerful children have a higher mortality risk across their lifespan. Without a stronger theoretical rationale for trait choice, we risk a fishing expedition in which chance associations will be found due to the sheer number of computed correlations. Even if some traits can be shown to have 'pervasive effects on social, sexual and familial life', such contemporary proximal effects may not translate into different long-term inclusive fitness outcomes.

If personality differences reflect adaptations then we would expect to find a multimodal distribution. Anisogamy evolved because there was an equal advantage in producing numerous small, cheap gametes or fewer large, expensive gametes. Once this cleavage began, there was no advantage in producing intermediate-sized ones. Disruptive selection should apply equally to individual differences as adaptations. We should expect to see a number of human 'types' rather than a continuous normal distribution. (Indeed the picture is even more complicated since humans vary not just on one trait but on five simultaneously, creating a near infinite range of individual differences.) The normal distribution of personality variation suggests not 'types' but a 'continuum' resulting from allelic variation over a number of genetic loci. Personality variations are expected to be polygenic in origin and, under selective neutrality, "genetic variation can be expected to be mainly additive". If ten coins (gene loci) are each flipped simultaneously the likely outcome is a normal distribution—the probability of ten heads (extreme introversion) or ten tails (extreme extraversion) is extremely low. (True, a similar distribution might be seen as a 'snapshot' under balancing selection. But that snapshot would have to be taken at precisely the time or place at which the forces favouring the two strategies were momentarily in perfect balance.)

If there is to be a search for function, I agree with the authors that we have been uncritical in taking the Big Five as the compass. These traits emerged from people rating themselves in terms nominated by another set of people (psychologists). The extent to which such traits are significant for molecular genetics or evolution—as opposed to human social perception—is debatable. Instead, the authors suggest that the search for adaptive significance might begin by identifying endophenotypes (specific biopsychological processes). Korte, Koolhaas, Wingfield, and McEwen's (2005) work provides a recent example of this approach. Across a range of species, they have identified two responses to stressors. 'Doves' show a strong HPA response but a lower SAM response while Hawks show the reverse pattern. These differences have been linked 'upstream' to genetic polymorphisms and neurotransmitter activity, and 'downstream' to manifest behaviours (fear, aggression, sensitivity to environmental threats).

Nonetheless I find the case for balancing selection suspicious on two counts. Firstly, as the authors note, the chief source of selection operating on humans has been conspecifics. While environments may show rapid and fluctuating alterations over time and space, this hardly seems to characterise human interactions. Why would there be sexual selection for anxiety or introversion at one point in time or history, but preference for the opposite qualities at another? Why would anyone at any time or place want an ally that was unreliable and duplicitous? Such questions bring me to my second point, the ubiquitous Just-So story. The costs and benefits of extraversion, while providing a lively

topic for speculation, will not be solved by “much more research” in so far as we lack access to the variable social and environmental niches which putatively supported them. In place of stories, what Penke et al. (this issue) have very usefully provided is a profile, linking behaviour genetic to population genetic parameters, which can guide our search for the evolutionary relevance---or irrelevance---of personality.

An Evolutionary Ecologist’s View of How to Study the Persistence of Genetic Variation in Personality

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Abstract

Personality is commonly regarded to involve either “correlations among behavioural traits” or “consistent individual differences in behaviour across contexts”. Any evolutionary explanation for the existence of genetic variation in personality must therefore not only address why genetic variation in single behavioural traits is maintained but also why behavioural traits are correlated, and why individuals show limited behavioural plasticity.

Penke et al. (this issue) propose a framework for studying genetic variation in personality. Their framework is important because it outlines why genetic variation in behaviour – a key characteristic of personality – might exist, but is, yet, incomplete. In this commentary I outline why.

Although many definitions of personality exist (see Réale, Reader, Sol, McDougall, & Dingemanse, 2007, for a recent overview), it is commonly agreed that personality involves either “genetic correlations among behavioural traits expressed in different environments” (when viewed from a 'character state' perspective; Via & Lande 1985; Via et al., 1995), or “consistent individual differences in behaviour across contexts” (when viewed from a 'reaction norm' perspective; de Jong, 1995; Via et al., 1995). Viewed from a character state perspective (which is not explicitly discussed by Penke et al., this issue), genetic

variation in personality therefore does not exist if genetic correlations among behavioural traits are all very weak or absent (Figure 1a) but does exist if genetic correlations are tight (Figure 1b). Viewed from a reaction norm perspective, genetic variation in personality does not exist when both the gene × environment interaction (G×E) between a behaviour expressed in different environments is very strong (Figure 1c) *and* the cross-environment genetic correlation is weak (as illustrated in Figure 1a) but does exist if a trait is both heritable in different environments *and* exhibits no (or very weak) G×E (Figure 1d; resulting in a tight cross-environment genetic correlation as shown in Figure 1b). Consequently, understanding why genetic variation in personality exists requires insight in evolutionary mechanisms that either (i) simultaneously promote persistence of genetic variation in single behaviours *and* genetic covariation between behavioural traits (Figure 1b) and/or (ii) simultaneously promote persistence of genetic variation in a single behaviour *and* the existence of limited plasticity of the behaviour across contexts (Figure 1d). Penke et al.'s framework addresses mechanisms explaining genetic variation in a single trait; it does not addresses adaptive explanations for why traits might be correlated or why individuals show limited plasticity.

- insert Fig. 1 here -

An evolutionary ecologist's research agenda for studying genetic variation in personality would, depending on the chosen approach, thus include the following topics. If one adopts the character state approach, a fruitful agenda would start by (i) measuring multiple behaviours on individuals with known pedigree relationships, (ii) revealing the genetic structure of personality by estimating additive genetic variances (V_A) and covariances (so-called G-matrix) from these data (see Lynch & Walsh, 1998), (iii) measuring the fitness consequences of personality where selection pressures favouring correlations among traits should explicitly be examined (Dingemanse & Réale, 2005; this crucial step is missing from Penke et al.'s framework), and finally (iv) predicting how the G-matrix might evolve in response to selection (Steppan, Phillips, & Houle, 2002) – instead of using solely verbal arguments. Such data would reveal whether a combination of balancing and correlational selection does indeed maintain genetic variation in personality.

If one adopts the reaction norm approach, the research agenda would start by explicitly considering that reaction norms are characterised by slopes and intercepts that might both evolve (de Jong 1990). In contrast, Penke et al. seem to regard personality as a collection of fixed reaction norms that cannot evolve. A fruitful approach would continue by (i) measuring behaviour of the same individuals over multiple contexts (using a set of

individuals with known pedigree relationships), (ii) obtaining estimates of intercepts and slopes for each individual that would then be used to estimate V_A in both parameters (Lynch & Walsh 1998), (iii) measuring how the intercept and slope of an individual (and potentially their interaction) affect fitness (Van Tienderen 1991; Scheiner & Berrigan 1998), and finally (iv) assessing whether the observed selective pressures would indeed maintain genetic variation in personality. Evidence for disruptive and/or fluctuating selection on intercepts in combination with stabilising selection on slopes would provide evidence in favour of Penke et al's balancing selection hypothesis.

Penke et al. simply invoke constraints on plasticity as an explanation for consistency of behaviour over contexts. Recent studies, however, show that genetic correlations (like those that cause personality) are rarely fixed and can easily change sign across populations or environments within populations (Sgro & Hoffmann, 2004). Penke et al's constraints view might thus prove invalid. Furthermore, even genetic correlations that are highly preserved (i.e. exist in many taxa) can often easily be broken by means of artificial selection (Beldade, Koops, & Brakefield, 2002), suggesting that genetic correlations (like those that cause personality) might instead have evolved because natural selection favoured associations between traits (Bell, 2005; Dingemanse & Réale 2005). The fact that individual variation in behaviour exists in a wide range of taxa (Gosling, 2001; Réale et al., 2007) should therefore not necessarily be viewed as evidence in favour of the view that constraints on behavioural organisation hamper adaptive evolution of behaviour. Instead, natural selection may have favoured the evolution of limited behavioural plasticity while simultaneously maintaining individual variation (Dall, Houston, & McNamara, 2004; McElreath & Strimling, 2006).

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Consilience is Needed, and Consilience Needs Bipartisan Expertise

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Abstract

Despite a common overarching home of biology, evolutionary psychology and behaviour genetics have not fostered mutual exchange. The article combines expertise in evolutionary genetics and personality theory with didactic skill and makes a strong argument for two mechanisms of evolutionary genetics to explain the persistence of genetic variation in intelligence and personality, thus contributing considerably to interdisciplinary consilience.

A few years ago the late Linda Mealy (2001) likened evolutionary psychology and behaviour genetics to two sisters of about the same age. Both occupy two different niches within the family with different interests and optimal resource extraction: What is chaff to one sister is wheat to the other. Evolutionary psychology tells stories about human universals and trashes individual differences, whereas behaviour genetics cherishes just these differences. Sister behaviour genetics has exuberantly been telling an old aunt called personality psychology exciting new findings, like that genes are important and that the magic of family influence is just an urban legend. The aunt dislikes genes and considers it improper to talk about such infamous things in front of others. But the other sister also lacks good manners because she retells the kind of stories which the aunt had overheard in her childhood from old relatives called Charles and Herbert, and these stories were considered off-limits as she had learned when she got a bit older. As all three women vie for outside attention to their good looks there is less than complete harmony despite the thick-blooded family ties. Godfather Edward Wilson, a big-name salesman for a cure-all called Consilience, occasionally drops in and recommends his remedy.

The authors of the target article offer a remedy, one with several active ingredients. There is brief but excellent to-the-point primer of genetic variation, optimal for the reader

interested in personality theories but not an updated expert in evolutionary genetics. Secondly, the article reviews the unsatisfactory previous attempts to reconcile Fisher's dictum that selection winnows out alleles with highest fitness, thus removing all genetic variation in the long run, with the observation of heritabilities galore. The previous conclusion by Tooby and Cosmides (1990) that heritable variation signals a lack of adaptive significance has been indigestible for most evolutionary psychologists because it tried to entice us to ignore individual differences and thus forget about personality as a worthwhile subject from an evolutionary perspective.

Thirdly and most importantly, the authors delve into the evolutionary genetics of personality and argue skillfully and persuasively why, of the various possible genetic mechanisms, mutation-selection balance is the prime candidate to explain genetic variance in general intelligence, and balancing selection by environmental heterogeneity the prime candidate to explain variance in personality traits. To bolster these arguments, predictions are derived from the theory of evolutionary biology and evolutionary genetics, currently available data are mustered, and clear judgements are offered. Suddenly, several loose ends in our theorizing might become connectable: different heritability estimates and different proportions of non-additive genetic variance for general intelligence and personality dimensions; different impact of shared environment on intelligence and on personality dimensions; inbreeding depression and outbreeding elevation for intelligence but not for personality; generally higher heritability for sexually selected than for naturally selected traits.

Most helpful to evaluate systematically the possible genetic mechanisms in genetic variation is Table 1 in Penke et al. (this issue). Admittedly, the entries are ordinal at best and vague at worst, but they suffice to navigate the reader through the sometimes demanding subject matter and provide a different vantage point, and they suffice to evaluate by comparative evidence. The watershed model has its own charm and merits, not the least because it may help to reconcile approaches in evolutionary anthropology with those in evolutionary psychology. The former insist on fitness measures and settle as far downstream as possible. The latter, unless they commit betrayal of their discipline, have to find their niches upstream along tributaries. The model makes salient that both approaches are working with the same body of water, in fact with the same water.

In the last decade evolutionary approaches and adaptionistic theorizing have finally gained increased acceptance within the psychologies of continental Europe (Euler & Voland, 2001). The target article exemplifies for personality psychology how promising and gainful

an interdisciplinary approach with bipartisan expertise can be and how much it can contribute to consilience of estranged disciplines.

Genetic Variance and Strategic Pluralism

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Abstract

Penke et al. (this issue) have written a provocative paper on the evolutionary genetics of personality, ascribing the maintenance of genetic variation in personality to balancing selection and in cognitive abilities to a balance between mutation pressure and directional selection. Some of the theory and evidence presented appears supportive, but both the theoretical predictions and the supporting empirical evidence remain tentative.

Penke et al. (this issue) (PDM) have written a provocative paper on the evolutionary genetics of personality. The ideas presented are extremely exciting and worth further research, but we have certain reservations about some of the conclusions drawn from the existing body of theory and evidence.

After making and evaluating differential predictions about the expected structure of the genetic variability in traits that would be maintained by neutral selection, balancing selection, and mutation-selection balance, respectively, PDM draw the following three major conclusions: (1) that genetic variability in personality traits is maintained by balancing selection, (2) that genetic variability in cognitive abilities is maintained through mutation-selection balance, and (3) that neutral selection does not adequately explain the observed genetic variability in either personality or cognitive ability. While we are inclined to agree with them on all three major points, although perhaps for different reasons, we found that some of the logical inferences made in PDM's argument were difficult to follow and require further clarification. The problem stems, in part, from ambiguities and incomplete equivalences in the terminology used by PDM and in relation to the original sources cited.

PDM argue that there are high absolute values of additive genetic variance in traits closely related to fitness (termed “fitness traits” by Merilä & Sheldon, 1999) because fitness and life history traits are potentially affected by mutations at a large number of genetic loci. Therefore, even though fitness traits might be under strong directional selection, a large absolute value of additive genetic variance can be maintained by the opposing action of mutation pressure. Thus far, we agree with them. However, PDM also assume that fitness-relevant traits are necessarily and exclusively subject to directional selection as opposed to balancing selection. In contrast, we argue that any traits under balancing selection must also be closely connected to resultant fitness. For example, as PDM note, balancing selection has been proposed by ourselves and others as an explanation for the maintenance of genetic variability in life history traits. Although life history traits are definitely relevant to fitness, alternative reproductive strategies might nonetheless have equal fitness payoffs, especially within complex social ecologies.

PDM equate “downstream” traits with “fitness” traits. Because PDM argue that fitness-relevant downstream traits are subject to a balance between mutation pressure and directional selection, they go further to imply that downstream/fitness traits are also less likely to be subject to balancing selection, as indicated by their high levels additive genetic variance. We do not understand why this must necessarily be so. The concept of a downstream trait with high fitness relevance does not seem useful to us for distinguishing between directional and balancing selection. The foundation upon which to make strong differential predictions about the structure of genetic variability between mutation-selection balance and balancing selection therefore seems fragile. Similarly, it is unclear to us why additive genetic variance should tend to be depleted in traits under balancing selection.

PDM’s multiple conflation of downstream traits, fitness traits, and life-history traits with strong and exclusively directional selection is troubling because human life history strategy has been shown to be significantly related to personality traits and could therefore be partially under the control of balancing selection, as PDM acknowledge (Figueredo et al., 2005 a,b). They cite us as observing that a “fortuitous side-effect” of variation in life history strategy and personality “is that such variation reduces within-group and between-group competition by allowing individuals and groups to fill different socio-environmental niches”. In fact, the predictions that we made were stronger and more specific: (1) that selection for variation in life history strategy may ultimately be the principal driving force behind selection for variation in personality, and (2) that partial release from intraspecific competition within social groups is the evolved adaptive function of this variation, not merely a “fortuitous side-effect”. In a separate twin study (Figueredo, Vásquez, Brumbach,

& Schneider, 2004; Figueredo et al., 2006), we have also shown a substantial genetic correlation (r_g =.78) between a higher-order personality factor and a multivariate composite of a wide array of cognitive and behavioral indicators of life history strategy. Furthermore, we have reported a substantial broad-sense heritability (h^2 =.65) for this general life history (K) factor. Unfortunately, the twin study did not contain associated data from other (non-twin) siblings, so we were not able to estimate the relative proportions of additive and non-additive genetic variance.

PDM state that significant absolute and proportional levels of non-additive genetic variance indicate that a given trait has had a recent history of selection. We are unclear as to what type of selection is meant here, but we suspect that directional selection is implied. PDM also state that high levels of non-additive genetic variance (specifically dominance variance) are observed in personality traits and that this variability is only explainable by balancing selection because dominance variance levels are expected to be in the middle range for traits under mutation-selection balance, but higher under balancing selection. Since traits with a recent history of selection and traits under balancing selection are both predicted to have significant levels of non-additive genetic variance, we are unclear what, if any, differential predictions there are about the levels of non-additive variance in traits under directional versus balancing selection.

In sum, although we sympathize with their final position, we are skeptical about the apparent certainty with which PDM present their differential predictions as purportedly reliable criteria for discriminating between the alternative mechanisms for maintaining genetic variability. In the literature cited by PDM (e.g., Crnokrak & Roff, 1995; Merilä & Sheldon, 1999; Stirling, Réale, & Roff, 2002), these are treated more tentatively as working hypotheses, for which the evidence is often equivocal, than as empirically well-substantiated observations. In their response to these commentaries, PDM should therefore: (1) better elucidate the inferential steps they made in reaching their conclusions regarding the ultimate causes underlying the maintenance of genetic variability in personality and cognitive abilities, and (2) specify the empirical evidence supporting these conclusions, explicitly distinguishing empirical data from theoretical conjecture.

Beyond Just-so Stories towards a Psychology of Situations: Evolutionary Accounts of Individual Differences Require Independent Assessment of Personality and Situational Variables

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Abstract

Evolutionary theory is perhaps better used as a brake on theory than as a source of "just-so" stories of the origin of characteristics. The target article admirably employs evolutionary theory to test competing models of the maintenance of individual differences. Areas needing further development include separating personality from situational variables, rather than confounding them, and developing a psychology of situations.

Many personality and social psychologists are skeptical about the relevance of evolutionary theorizing to psychology. Why? It is not because they doubt the general truth of evolutionary theory. Rather, the skepticism stems from the proliferation within evolutionary psychology, especially in its early days, of "just-so" stories reminiscent of the tales by Rudyard Kipling that explained how the whale got its throat, how the camel got its hump, and so forth. Kipling invented these stories by observing interesting aspects of nature and then letting his imagination run wild. Evolutionary psychologists have sometimes proceeded the same way, with the result that they seemed ready to explain

anything from preference to salty foods to spousal murder. While nearly all the evolutionary stories were interesting, and an (unknown) number of them may even be true, their sheer number and variety can feed rather than repel skepticism, and help to fuel wide ranging critiques (e.g., Gould & Lewontin, 1979). The basic problem with these stories, besides their number, is their origin in a strategy of beginning with a known phenomenon and reasoning backwards to a cause – not unlike Kipling's.

But there is another way to use evolutionary theory. Rather than as a source of limitless explanatory theories for the origin of anything, evolutionary psychology can profitably be used as a *brake* on theorizing. If one accepts that the diversity of life, including human psychological life, is a product of evolutionary processes, then certain other theoretical positions become less tenable. For example, some versions of psychoanalysis posit the existence of a built-in drive in all persons towards death and destruction, including self-destruction. Is this idea plausible from an evolutionary perspective? For a very different example, some psychologists who study thinking and problem-solving argue that the human mind is fraught with basic design flaws. The many experiments demonstrating how people may systematically and grossly distort certain kinds of information are clever and sometimes entertaining, but is the idea of an information processing system flawed at the level of its basic design evolutionarily plausible (see Funder, 1987, 2000; Gigerenzer, Todd & the ABC Research Group, 1999)?

The target article follows this second approach, evaluating three models of the maintenance of individual differences in psychological attributes according to evolutionary plausibility. This approach leads the authors to several interesting conclusions, including a compelling description of the basic difference between attributes of ability and personality, a distinction that has been difficult to make on other grounds. Of particular interest is their explanation of how individual differences in personality can be maintained through the simultaneous existence of environments in which different levels of different traits are most adaptive. For example, exuberant extraversion might be adaptive in an environment that is abundant and relatively risk-free, whereas a more restrained introversion might promote survival under impoverished or dangerous circumstances. While on the whole their analysis is compelling, further development is needed in two respects.

One is the authors' touting of "individual reaction norms" as preferable to main-effect personality traits. Individual reaction norms are described as similar to Mischel and Shoda's (1995) CAPS model in which each individual's personality is described in terms of his or her if-then connections between situational stimuli and behavioral responses. This model has several shortcomings, including its startling resemblance to Watsonian (pre-Skinner) S-R behaviorism, the general statistical weakness of interactions compared to

more robust main effects (which the target article mentions), and the dilemma the model presents between characterizing individuals in terms of idiographic patterns (one for every living person) or boiling them down into a relatively small number of “types” – a problematical approach at best (see Asendorpf, 2002; also Funder, 2006, in press).

For present purposes the most important difficulty with individual reaction norms, as defined, is that they may contradict the purpose for which they are advocated. The authors persuasively argue that personality traits can be differentially adaptive under different circumstances. Thus, to repeat their most simple example, an extraverted person is well-suited to take advantage of a safe environment while an introvert may survive better in a dangerous one. But notice how this example – and others presented in the paper – assumes a *main effect* of extraversion-introversion, not an interaction with safety-dangerousness. An individual’s degree of extraversion-introversion is a general or average tendency and individuals at both ends of the dimension continue to exist because each style is adaptive in different environments. But if instead traits are conceived as built-in interactions, why not just evolve a tendency to be extraverted if the situation is safe and introverted if dangers are afoot? The explanation of the survival of individual differences in personality traits as a result of their varying adaptive implications in different environments only works when the traits are thought of as main effects rather than interactions. More generally, the concept of a person-environment interaction is clearer and more analytically tractable when the two constituent terms are kept separate (Funder, in press; Reis, 2007).

A second and related observation is that further research on the interactions between traits and/or genotypes on the one hand, and environmental properties on the other, is at present sorely handicapped by the lack of means for conceptualizing and measuring environments. Situations as presented in expositions of the CAPS model, for example, are almost (but not quite) always described hypothetically, as for example, “Situations 1-6” (Mischel & Shoda, 1995, p. 247). This kind of labeling is presumably promissory to someday providing concrete descriptions, and dimensions for description, of situations. The description of psychological environments (or situations) is perhaps even more important to fulfill the potential of the analysis in the present paper, to describe the circumstances under which different traits, or even aspects of incipient psychopathology, are more and less adaptive. So far we have a small number of very interesting examples, some of which are hypothetical. What we need next are data, and means to gather those data. We need new measuring tools, and a psychology of situations (Wagerman & Funder, 2006).

Life History Theory and Evolutionary Genetics

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Abstract

Penke et al. (this issue) argue that evolutionary genetics offers important insights into the fundamental nature of personality—how people adaptive adjust to their life circumstances in particular ways, as well as failures to adapt. I strongly endorse this enterprise. It is particularly promising, I suggest, when embedded within life history theory, a broad evolutionary framework for understand selection on organisms.

Almost a century ago, Fisher (1918) famously showed how, given Mendelian inheritance, quantitative variation can be partitioned into forms of genetic and environmental variance, thereby laying foundations for both quantitative genetics (e.g., heritability estimation) and evolutionary genetics. Whereas, within biology, these topics are intertwined (e.g., Crow, 1986), most quantitative behaviour geneticists and personality psychologists have shown little interest in evolutionary genetics. I applaud Penke et al.'s efforts to remedy this neglect.

Many biologists (e.g., Houle, 1991) contextualize evolutionary genetics in a broad view of selection on organisms, life history theory (LHT). LHT has deep roots in evolutionary biology (for an overview, see Kaplan & Gangestad, 2005) and now pervades adaptationist theoretical analysis (e.g., of sexual selection: e.g., Kokko, Brooks, Jennions, & Morley, 2003; biological signals: Getty, 2006; immune function: McDade, 2003; patterns of aging: e.g., Kirkwood, 1990). My commentary touches on how, jointly, LHT and evolutionary genetics can shed light on the adaptive and maladaptive nature of personality variants.

Life history allocations. Organisms are designed by selection to harvest energy and convert it into fitness-enhancing activities. Within lineages and their niches, designs that do so most proficiently are selected (e.g., Charnov, 1993). A problem that designs must solve is how to efficiently allocate resources to the development and operation of the

organism's many fitness-enhancing features. At optimum performance, the marginal value of allocation (effectively, the effect on fitness of the last unit of allocation) to each feature should be equal. (Otherwise, reallocation could increase fitness.) Optimal allocation changes across the lifecourse and with conditions (e.g., skeletal growth and brain development may be particularly important early in life, allocation to reproductive traits may anticipate the end of growth, optimal allocation to immune function increases with infestation). Selection accordingly shapes organisms' characteristic life histories.

Implications for directional and stabilizing selection. Virtually no feature comes for free; a feature's development and maintenance entails opportunity costs. Hence, one can overspend even on "good" traits (e.g., brain function supporting IQ, immune function, DNA repair). Energy-rich diets in modern cultures don't overcome the problem, as metabolic and developmental processes evolved in leaner conditions impose constraints on proficient allocation of resources in real developmental time. Hence, most traits are (at least partly) under stabilizing selection; intermediate trait values are favored, whereas extremes are disfavored. Consider height. Extreme tallness or shortness may be selected against (see Nettle, 2002), partly because really tall people may have overallocated to growth, whereas short people may have underallocated to it.

Mutations typically diminish fitness because they reduce the proficiency with which organisms garner and allocate resources, and in at least a couple of ways. Mutations may produce inefficiencies in processes that build fitness-enhancing traits. They can also yield non-optimal allocation. Some extreme variants on traits under stabilizing selection (e.g., extreme tallness and extreme shortness) reflect mutation-induced non-optimal allocation: Some mutations lead to overallocation to the trait, others to underallocation (e.g., Houle, 1991).

Mutation-selection balance, then, doesn't only apply to traits under directional selection (see Penke et al., this issue); it can also explain genetic variation on traits under stabilizing selection (e.g., Crow, 1986). The latter tend to have *low* additive genetic coefficients of variation (CVAs), despite high h^2 (Houle, 1992; Pomiankowski & Møller, 1995). The CVA of height is generally less than CVAs of fitness traits (e.g., Miller & Penke, 2007). Brain size too possesses a low CVA (Miller & Penke, 2007). And some personality variation may be maintained by mutation-selection balance under stabilizing selection.

For some traits under (partial) stabilizing selection, however, the optimum value may be higher than the mean because, once again, some mutations (and other fitness-reducing events, including environmental ones) may reduce ability to develop fitness-enhancing

traits. A classic example is clutch size in birds: Although both small and very large clutch sizes are disfavored (the latter because they overstretch parents' abilities to care for offspring), the fittest parents can produce clutches larger than average (see Parker & Begon, 1986). Similarly, optimal height may be greater than average (Nettle, 2002). PDM imply that IQ has ancestrally been linearly related to fitness, but the low CVA of brain size (partly reflecting IQ) suggests it may be like avian clutch size: partly under stabilizing selection, with the optimum greater than the mean, but less than the high end of the range in IQ.

Reactive heritability. Selection may design organisms to adjust their developmental and behavioral strategies based on their particular circumstances, should those circumstances affect the payoffs of strategies. Selection accordingly shapes phenotypic plasticity and norms of reaction (Houston & McNamara, 1992). Plasticity explains, however, not only to environmental variation in traits. If circumstances themselves reflect genetic variation (e.g., compromises in condition due to mutations), so too do outcomes of strategy-adjustment. PDM allude to this phenomenon, albeit implicitly, when they discuss the idea that costly, sexually attractive signals evolve to reflect genetic variance in condition. When allocating optimally, individuals in best condition allocate more resources to these traits than do individuals in poorer condition (Rowe & Houle, 1996).

More generally, in long-lived species such as humans, individuals in poor condition may invest proportionately more in survival and less in reproductive traits that entail costs on immediate survival (e.g., Ellison, 2003). Accordingly, heritable variation in condition may translate, through adaptive adjustment, in differences in patterns of a range of phenotypic traits. For example, one life history view of the endocrine systems in which female estrogen and male testosterone are involved is that they have been shaped to adaptively modulate allocation to reproductive traits (e.g., female estrogen promoting current fertility and allocation to gynoid fat deposition; male testosterone promoting traits ancestrally important in mating competition, e.g., muscularity; see Ellison, 2001, 2003). Some variation in traits affected by reproductive hormones, then, may reflect condition-dependent strategy choice, not allelic variation in genes directly affecting hormone production or receptor densities. (Perhaps relevant is the recent finding that prepubertal boys of average IQ tend to have higher testosterone levels than boys of *either* very low *or* very high IQ; Ostatníková et al., 2007.)

Sum. By itself, heritability estimation reveals little about core personality, "psychophysical systems that determine (an individual's) unique adjustment to his environments" (Allport; cited by Penke et al., this issue). As these authors make clear, identifying the evolutionary

forces responsible for variation *can* yield insights into the nature of adaptation and maladaptations represented by personality variants. The enterprise may be particularly promising when embedded within a life history framework.

Behaviour Genetics' Neglected Twin: Gene-Environment Correlation

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Abstract

The target article posits that the driving force behind balancing selection is gene-environment interaction (GxE) that describes environmental control of genes. It is argued that GxE is insufficient to maintain genetic variability and that the concept of gene-environment correlation or genetic control of the environment leads to different conclusions regarding mental illness and hierarchical personality models.

Penke et al. (this issue) make a strong, logical argument that observed individual differences in personality are a reflection of genetic variability caused by balancing selection. Their argument relies heavily on the behavioural genetic concept of gene-environment interaction (GxE) and recent empirical research that has shown to exert a major influence in personality and psychopathology. GxE occurs when genotypes are differentially expressed when exposed to varying environmental conditions. It is argued that such genetic variability is maintained in a population because it confers fitness advantages by allowing organisms to adaptively react to different environmental conditions or – to use their term – niches.

However, the role of GxE as the primary mechanism for balancing selection is insufficient to explain genetic variability. This becomes clear when their arguments are used to try to explain mental illness and the genetic basis underlying the hierarchical structure of personality. Beginning with mental illness, they argue that mental illness is a consequence

of genetic variants no longer fitting environmental conditions so that "…modern societies produce mismatches between heritable temperaments and available niches".

Explaining Mental Illness. It follows that mental illness exists simply because humans cannot reproduce fast enough to keep up with environmental change and these variants survive because they have not had a chance to be selected out of the population. However, it can also be argued that such genotypes are maintained due to improvements to health care and because attitudes toward the mentally ill ensure these individuals survive to reproduce. This is a form of gene-environment interplay called gene-environment correlation (r_{GE}).

Gene-environment correlation refers to the process in which underlying genetic factors influence the probability of exposure to specific events – simply put, the genetic control of exposure to the environment. Plomin, DeFries, and Loehlin (1977) discussed three general types: passive, active, and reactive. Passive genotype-environment correlation occurs because children share heredity and environments with members of their family and can thus passively inherit environments correlated with their genetic propensities. Reactive genotype-environment correlation refers to experiences of the child derived from reactions of other people to the child's genetic propensities. Active genotype-environment correlation is known as "niche-building" or "niche picking" (Plomin, DeFries, & McClearn, 1990, p. 251) and refers to individuals actively selecting or creating environments commensurate with their underlying genetic propensities.

Assuming that some form of r_{GE} exists, its operation maintains genetic variability because these genes are operating in an active, passive or reactive manner to create all of the varied environments required for expression. This also helps to clarify some evolutionary psychological theorizing on mental illness that attempts to identify fitness advantages for mental illness. Under this model, mental illness has no fitness advantages and exists as a true pathology. In short, r_{GE} creates "stably unstable" environments that would maintain genetic variability for psychopathology. It should also be noted that for normal personality and behaviour, r_{GE} provides a powerful alternative explanation for genetic variability underlying this range of behaviour.

Hierarchical Structure of Personality. What influence does GxE have on the covariance of traits, and by extension, hierarchical models of personality? The authors suggest that the context-dependent nature of two traits can be used to determine if they are in a pleiotrophic relationship - indexed by a positive genetic correlation (r_G) – that results when

both respond within the same general reaction range when exposed to the same environments. If they do not share a common genetic basis, then the two traits can react in opposite ways – resulting in a negative genetic correlation. Thus, the absence of sign or valence changes across environments is a necessary condition for the existence of superordinate personality domains.

This is problematical for two reasons. First, what is important to estimating pleiotrophy – that the authors consider the central basis of superordinate traits - is not change in valence but rather the magnitude of r_G. A zero r_G is far more informative regarding the presence of shared genes than the change in valence. Moreover, demonstrating no change in the valence of r_G across environments as a necessary requirement for pleiotrophy is really an artificial and ecologically invalid consequence of hypothesized reaction ranges whose breadths are not broad enough to encompass zero as the midpoint.

Second, basing decisions on which traits are included as part of a domain (a version of the classic factor definition problem) based on reaction ranges may lead to erroneous conclusions for the reasons outlined above and because of potentially unaccounted for r_{GE} effects that can be misread as GxE (see Purcell, 2002). Finally, the authors' theory assumes that personality hierarchy is imposed by the action of genes shared across traits. Through the mechanism of r_{GE}, however, environments conducive to maintaining a particular hierarchy also play a role.

Recognizing the interdependence of genes and the environment (see Rutter, 2007) and the ability to specify mechanisms such as GxE as a driver of balancing selection is a major step forward. However, there are other effects, such as r_{GE}, that need to be incorporated into the theory that balancing selection maintains the genetic variability that we observe as individual differences in behaviour.

Don't Count on Structural Pleiotropy

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Abstract

Penke et al. (this issue) address the evolution of personality, articulating many insightful and provocative ideas. They do not, however, give enough attention to the role of G-E correlation in the processes they outline. Thus they underestimate the difficulty of establishing the existence of structural pleiotropy and overestimate its ability to help us in understanding the development of personality.

In their insightful and provocative paper, Penke et al. (this issue) use the term "GxE interaction" to refer to the adaptive fit of an organism to its environment. They describe this adaptive process as being comprised of natural selection, or relative reproductive success, and phenotypic plasticity, or the potential for a given genotype to produce different phenotypes in different environments. They note that phenotypic plasticity is not complete, even for behavioral traits: the organism cannot adapt perfectly and instantly to all environmental demands because the cues to optimal adaptation provided by the environment are too unreliable. They point out that, to the extent that environmental cues are reliable, natural selection acts over time to limit phenotypic plasticity, and suggest that what phenotypic plasticity remains largely reflects genotypic differences that persist in the population. This is, of course, possible, but the very unreliability of environmental cues makes it unnecessary. The same genotype could respond differently to different environmental circumstances simply because there are enough ways in which the environment varies that natural selection cannot operate to remove the phenotypic plasticity.

In population genetics, the term "GxE interaction" has a specific technical definition as genetic control of sensitivity to different environments, or, equivalently, environmental control of expression of genetic influences (Kendler & Eaves, 1986). The adaptive fit of an

animal (human or otherwise) to its environment is always more than this: the animal has some choice of exactly what environment it faces. This is captured by another population genetics term, "G-E correlation," which refers to genetic control of exposure to different environments, or, equivalently, the environmental control of gene frequency (Kendler & Eaves, 1986). For example, when food is scarce in one area, animals will expand the range over which they search for it. There may be genetically influenced individual differences in the extent to which this is true, but the animal that wanders furthest in search of food may have the same reproductive success as one that does not wander as far but has the metabolic efficiency to survive better on less food. Because adaptation involves both GxE interaction and G-E correlation, it would be helpful to use a term that encompasses both. "G-E transaction" is one such term.

G-E correlation can be completely passive, as when parents transmit both genetic influences and environmental circumstances to their offspring. But often G-E correlation is active: the individual either directly seeks an environment or behaves in a way that elicits certain kinds of environmental responses. As with phenotypic plasticity, individuals cannot select their environments completely at will. Still, the facts that particular genotypes can produce more than one phenotype and that individuals can select their environments to some degree mean that GxE interaction and G-E correlation are often closely inter-related. This relation takes place because proper measurement of the environment often involves recognition of individual differences in response to that environment, individual differences that generally show genetic influence.

For example, measurement of the environment when food is scarce would mean recognizing that some animals are more affected by the relative lack of food than others, perhaps by measuring individual levels of caloric deprivation. But animals with relatively lower levels of metabolic efficiency will be more motivated to expand the range over which they search for food, creating at least statistical if not genotypic pleiotropy between metabolic efficiency and food-seeking range among those animals. Natural selection will tend to have its greatest effects on those who have both low levels of metabolic efficiency and low tendencies to explore in search of food. Genetic influences on food-seeking range will be expressed most strongly among those with low metabolic efficiency, a GxE interaction. The G-E correlation will also be greatest among these animals, because of the selection process involved in food-seeking range. The ways in which G-E transactions are related are discussed in detail in Johnson (2007).

Penke et al. (this issue) correctly point out that phenotypic plasticity is limited because the environment does not reliably signal the most adaptive behavioral strategy. It is this unreliability of environmental cues in the presence of phenotypic plasticity that implies that genetic influences on a trait do not necessarily mean genotypic differences at particular loci. This is because, for any one gene in a genotype, the other genes function as part of the environment. In combination with the ability of an animal to select its environment, this has important implications for the norm of reaction model Penke et al. (this issue) articulate. The norm of reaction concept was developed with organisms under controlled breeding and environmental conditions, and in naturalistic settings the concept breaks down in important ways. For example, in the simplified terms of Penke et al.'s Figure 2b, people with genotype A may avoid environment Z completely, and people with genotype B may be over-represented there. This implies that genetic correlations observed across the environmental range may not reflect similarities and differences in genotype in any predetermined, formulaic way even when the correlations do not change sign.

Penke et al. (this issue) suggest that structural pleiotropy, or functional, physiological, or developmental links between genetic influences on different traits that constrain independent phenotypic expression of the traits in all environments, may help us to understand personality development. The ability to select our own environments makes it likely that structural pleiotropy is rare for personality traits, and that it is very hard to be sure that we have observed it even when it does exist. This may explain the relative weakness of the structural hierarchy of personality traits that depends on structural pleiotropy, as indicated by the genetic correlations between factors of the five-factor model that are theoretically independent (Jang, Livesley, Angleitner, Riemann, & Vernon, 2002; Jang et al., 2001), problems that show up in the phenotypic models of the hierarchy as well (e.g., Roberts, Bogg, Walton, Chernyshenko, & Stark, 2004). Though it would be nice if we could rely on structural pleiotropy to understand personality and its evolution, it seems likely that we will have to make do largely without it.

Standards of Evidence in the Nascent Field of Evolutionary Behavioral Genetics

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Abstract

Penke et al. (this issue) argue that the genetic variation underlying cognitive abilities is probably due to evolutionarily recurrent, deleterious mutations at the thousands of loci that could potentially affect cognitive development, whereas the genetic variation underlying personality is probably due to balancing selection. This may well be correct, but I argue that some of the standards of evidence they forward are not well supported by evolutionary genetics theory. It is important at this early stage of evolutionary behavioral genetics to critically debate the standards of evidence that will help us distinguish between alternative hypotheses.

I applaud Penke et al.'s (PDM) attempt to understand the evolutionary processes that explain the genetic and environmental causes of variation in personality and cognitive abilities. Their paper is the most recent in a growing movement to use evolutionary genetics to bridge the gaps between behavioral genetics and evolutionary psychology (Gangestad & Yeo, 1997; Keller & Miller, 2006; Macdonald, 1995; Mealey, 1995; Miller, 2000b; Yeo & Gangestad, 1993; Yeo, Gangestad, Edgar, & Thoma, 1999)—an endeavor that can be termed "evolutionary behavioral genetics". In particular, PDM's framework is largely consonant with one that Miller and I recently forwarded regarding the evolutionary persistence of genetic variation underlying mental disorders (Keller & Miller, 2006), and so it is not surprising that I should mostly agree with their viewpoint. However, expounding upon our agreements would be a disservice to the type of critical debate that is important to scientific progress; this principle applies doubly to young scientific movements such as evolutionary behavioral genetics. Therefore, in this commentary, I endeavor to point out concerns I have with PDM's interpretation of data or theory, and forward alternative explanations that I do not feel have necessarily been laid to rest. Nevertheless, my

approach should not obscure the fact that, overall, my agreements with this paper far outweigh my concerns.

PDM's thesis is that cognitive abilities have been under directional (and probably sexual) selection over evolutionary time, and that recurrent mutations at a large number of loci account for the genetic variation underlying these abilities. They argue that personality, on the other hand, is more likely to have been under some type of balancing selection (and, in particular, probably frequency dependent selection), and so differences in personality have had fitness costs and benefits that cancel each other out over evolutionary time. This conclusion may very well be correct, but I do not think that some of the evidence marshaled in favor of this hypothesis is quite as clear-cut as PDM seem to imply. In particular, I am unconvinced that the genetic architecture of traits tells us much about the evolutionary mechanisms responsible for their variation.

PDM state that mutation-selection predicts greater additive genetic variation than balancing selection, and that the degree of non-additive genetic variation is highest for balancing selection, moderate for mutation-selection, and lowest for neutrality (PDM, Table 1). At the same time, many measures of personality appear to demonstrate high levels of non-additive genetic variation (Eaves, Heath, Neale, Hewitt, & Martin, 1998; Keller, Coventry, Heath, & Martin, 2005; Lake, Eaves, Maes, Heath, & Martin, 2000) whereas the genetic variation underlying cognitive abilities appears to be mostly additive in nature (e.g., Rijsdijk, Vernon, & Boomsma, 2002; but see also Pedersen, Plomin, Nesselroade, & McClearn, 1992). Do such findings lend support to the hypothesis that balancing selection accounts for the variation in personality whereas mutation-selection accounts for the variation in cognitive abilities? I do not think they do.

Several studies on non-human animals have found that traits most related to fitness tend to have high levels of additive genetic variation (as measured using coefficients of variation) (Houle, 1992; Price & Schluter, 1991) but even higher levels of non-additive genetic variation, resulting in low narrow-sense heritabilities of such traits (Crnokrak & Roff, 1995; Falconer, 1989; Roff, 1997). There is also convincing data that mutation-selection accounts for much of the genetic variation underlying such fitness related traits (Charlesworth & Hughes, 1999; Houle, 1992, 1998). Therefore, the evidence does not seem to support PDM's blanket assertion that mutation-selection predicts higher levels of additive than non-additive genetic variation—indeed, the opposite is probably true. That said, I should add that there is some, albeit imperfect, evidence that sexually selected traits in particular show higher levels of additive genetic variation compared to other fitness

related traits (Pomiankowski & Møller, 1995), a finding consistent with Miller's (2000a) and PDM's hypothesis that cognitive abilities have been under sexual selection. This may occur because selection favors mating signals that reveal as much additive genetic variation as possible (Pomiankowski & Møller, 1995).

I am also unconvinced that balancing selection generally leads to high levels of non-additive genetic variation (PDM's Table 1). Certainly some forms of it do—overdominance for fitness for example. But other forms of it—frequency dependent selection and temporal/spatial variability in the fitness landscapes, for instance—predict high levels of additive genetic variation. Thus, I would argue that the ratio of additive to non-additive genetic variation tells us little about the relative merits of mutation-selection versus balancing selection.

Finally, in keeping with the critical spirit of my commentary, I feel impelled to backtrack on an assertion that I made previously and one cited by PDM. Contra Keller et al. (2005), I am no longer convinced that observations of non-additive genetic variation necessarily make neutral explanations unlikely. It is true that traits that are closer to neutral evolutionarily (e.g., morphological traits) tend to show higher ratios of additive to non-additive genetic variation (Crnokrak & Roff, 1995; Mousseau & Roff, 1987) whereas traits under more intense selection tend to show lower ratios (Crnokrak & Roff, 1995; Falconer, 1989; Roff, 1997), but the rule is not hard and fast. The reason is that the detection of non-additive genetic variation is highly sensitive to scale—it depends on how the trait is measured. For example, twin studies find evidence for high levels of non-additive genetic variation underlying absolute skin conductance, whereas the genetic variation of "range corrected" skin conductance (a mere change in scale) appears to be purely additive in nature (Lykken, 2006). Along these lines, how are we to know the true scale along which psychological constructs, such as personality, are actually measured, or whether the micro-traits (or endophenotypes) underlying psychological constructs combine additively or multiplicatively?

I do not think that the genetic architecture of traits provides a very reliable clue as to the mechanism explaining their genetic variation. Fortunately, other pieces of evidence can better help us understand the mechanisms responsible for the genetic variation underlying a trait. Several of these are described in PDM (see also Keller & Miller, 2006): the numbers and allelic spectrums of loci affecting the trait, whether the trait shows inbreeding depression (although in addition to mutation-selection, overdominance for fitness can also cause inbreeding depression), the degree of assortative mating that occurs on the trait

(although assortative mating on deviations from the mean should also be considered if the trait could have been under stabilizing selection), and whether its expression depends on overall condition. The effects of paternal age, radiation, and trauma on the trait, all consistent with mutation-selection, provide additional clues. Furthermore, once an allele that affects trait variation has been identified using, for example, association methods, its base-pair sequence can provide important information regarding the relative merits of ancestral neutrality, mutation-selection, and balancing selection (Bamshad & Wooding, 2003; Otto, 2000).

PDM's paper is insightful and offers us plenty to consider. I find the argument that cognitive abilities have been under ancestral sexual selection quite compelling, but remain as yet unconvinced by, but open to, PDM's argument regarding the genetic variation in personality. In particular, I find Tooby and Cosmides (1990) hypothesis (personality variation is in part a byproduct of genetic variation that exists for reasons unrelated to personality), MacDonalds's (1995) hypothesis (personality is under weak stabilizing selection, such that fitness differences within its normal ranges are trivial) and Buss' (2006) hypothesis (personality is under weak directional selection, and its variation is a byproduct of mutational noise) all to be viable alternatives. My main disagreement with PDM is not in their broad conclusions, however, but rather in some of the standards of evidence they bring to bear on the issue.

The field of evolutionary behavioral genetics is young, and our first steps should be made with the circumspection befitting its fledgling nature. Much wasted time and effort can be averted if, at this stage, we remain wary of groupthink (Janis, 1972). For the sake of our nascent field, it is important to critically debate the standards of evidence that will help us distinguish between alternative hypotheses, and to refrain from forming consensus on major issues too readily.

Humans in Evolutionary Transition?

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Abstract

One shortcoming in this otherwise excellent article is a neglect of additional hypotheses as to the high heritability of behavioral traits that may have been exposed to directional selection. I point to some evidence that humans are in the midst of an evolutionary transition that may account for the genetic variation in such traits.

The target article urges bringing the power of modern evolutionary biology to bear on the variation observed in human behavioral traits. As the inauguration of this ambitious undertaking is long overdue, the target article should prove to be an indispensable reference for some time. The authors' treatment of non-cognitive behavioral traits is particularly cogent. I devote my allotted space to pointing out what I feel are misplaced emphases and premature judgments in their treatment of traits that plausibly have been under directional selection in our evolutionary past.

Citing Fisher's fundamental theorem of natural selection (1930) for the proposition that directional selection should deplete genetic variation, the authors then argue that a special explanation is required for the abundance of genetic variation that is observed in some behavioral traits. Their own special explanation bears some resemblance to the infinitesimal model: the loci underlying fitness-relevant traits are posited to be so numerous and small in effect that selection against deleterious mutants is extremely weak and thus ineffective in removing the additive genetic variance. I have two related quibbles with this hypothesis. First, the fundamental theorem does not concern itself with the ultimate genetic architecture of a trait at all. What the theorem actually says is that the change in mean fitness at any time ascribable solely to natural selection acting on allele frequencies is equal to the additive genetic variance in fitness at that time. To infer from this statement that directional selection should extinguish genetic variation is an extrapolation not entailed by the theorem itself. Readers interested in this point are advised to consult Frank and

Slatkin (1992), Edwards (1994), Crow (2002), and Grafen (2003). Second, regardless of the authority cited for it, the extrapolation does not necessarily follow. There are "sufficiently plausible" reasons for any given failure of directional selection to deplete the additive genetic variance other than the one given by the authors (e.g., Hill & Keightley, 1987). I now provide a partial account.

On the basis of their model, the authors predict the absence or rarity of deleterious alleles at intermediate frequency. However, this assertion that the enhancing alleles for fitness-affecting traits are ancestral and nearly fixed seems to be empirically contradicted by the large number of selective sweeps detected by recent genome-wide surveys. In their scan for long, high-frequency, derived haplotypes in the human genome, Wang, Kodama, Baldi, and Moyzis (2006) found 1,800 sites showing signals of strong and recent selection in or near known coding genes. One of the biological categories enriched for such signals is neuronal function. As their survey failed to detect selection at some loci where single-gene studies have documented selection with a high degree of confidence (e.g., Evans et al., 2005), these signals probably fail to capture the full extent to which selection has been acting in our species.

This extraordinarily large number of selective sweeps in progress reveals that humans are in the midst of an evolutionary transition. Given the absence of selective equilibrium, substantial genetic variation in any trait (including fitness) becomes compatible with several possible genetic architectures and evolutionary histories other than the one envisioned by the authors. This is because such parameters as the additive genetic variance depend on the initial distribution of allelic effects and frequencies. As the variance of a dichotomous random variable is maximized at $p = 0.5$, an architecture biased toward initially uncommon enhancing variants may show an *increase* in the genetic variance under directional selection. The large number of fitness-enhancing variants at intermediate frequencies in the human genome is certainly consistent with a bias of this kind. Such a bias may even be traceable to known developments in human evolutionary history. For example, Evans et al. (2006) have provided persuasive evidence that an adaptive variant of the brain development gene *MCPH1* was introgressed into the human gene pool from an archaic *Homo* lineage. Hawks and Cochran (2006) argue that such introgressive events have contributed substantially to the evolution of our species, as interbreeding can introduce many more adaptive variants within a given time span than mutation alone.

The authors urge a greater focus in association studies of cognitive abilities on still-rare deleterious mutations, perhaps present in a single population. This commentary sets forth

reasons to doubt that loci harboring variants of this kind account for nearly the entire observed genetic variance in these traits. Resisting the authors' proposal of an ancestral genome encoding a Platonic ideal of human adaptation that is inevitably disrupted by new and deleterious mutations of small effect (where variability in how much of this "mutational noise" is inherited accounts for individual differences in *g* and other ability factors), I suggest in its place a genome undergoing massive recent turnover in response to selection pressures that are as yet incompletely characterized. The kinds of variants that follow from the authors' proposal are no doubt numerous. But given the tumultuous picture of human adaptive changes that emerges from recent work, a more interesting goal with respect to the illumination of our evolutionary history may be to look for novel enhancing variants across the entire spectrum of frequencies in all populations. The few genes linked to IQ in family-based designs robust against the potentially confounding effects of population substructure all match one or more aspects of this pattern: enhanced IQ associated with derived variants, signs of selection, or intermediate frequencies in one or more populations (Comings et al., 2003; Plomin et al., 2004; Blasi et al., 2006; Gosso et al., 2006a, 2006b). Given the many ways in which genotype-phenotype association studies can fail, I do not take this relative paucity of results to be evidence of absence. In fact, I am optimistic that forthcoming empirical evidence will help resolve the main issue discussed in this commentary.

Personality Traits and Adaptive Mechanisms

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Abstract

The issues addressed in this paper are basic to the foundation of a science of personality. The integration of behavioral genetic and evolutionary psychology perspectives on personality has the potential to contribute to the integrated conceptual foundation that the field needs. The task that the authors seek to explicate – the factors contributing to genetic variability of personality traits – is an important component of this integration although only part of an evolution-informed model of personality.

In focusing on selective neutrality, mutation-selection balance, and balancing selection as explanations of genetic variability, the authors give short shrift to earlier explanations. Genetically based variability is a feature of most biological systems and structures. As Tooby and Cosmides (1990) pointed out in a seminal contribution, this variability does not appear to disrupt the functioning of these adaptive mechanisms. The genetic variability of "mental mechanisms" including traits does not at first glance appear different from that of other biological systems. Tooby and Cosmides hypothesize that this variation is due to variability at the protein level that does not affect the mechanism's function but does contribute to defence against pathogens. This argument is dismissed largely on the grounds that the alleles associated with the immune system are very different from those associated with personality systems. However, Tooby and Cosmedes argument is more subtle. The argument is not that genetic variability enhances the immune system responses but rather that protein variability creates an ever-changing substrate or micro-environment that makes it more difficult for pathogens to be successful or evolve around host defences. In a sense, sexual recombination creates minor "lesions" that produce variation independently of function. This parsimonious hypothesis views genetic variability in personality as part of overall variability in adaptive mechanisms. In this sense, genetic differences in sensation seeking or anxiousness do not differ greatly from genetically based differences in the size of a limb or other organ. The authors reject this idea asserting simply that the number of alleles involved in personality variation is far greater although it is unclear that this is the case with complex anatomical structures and physiological systems.

Penke and colleagues reject the pathogen defence hypothesis as part of their rejection of selective neutrality as the mechanism maintaining variability. The pathogen-defence mechanism requires that variability is adaptive with regards to the host's resistance but that the normal range of the personality phenotypes are equally adaptive so that no selection pressures occur at this level. They argue that the latter is unlikely because of non-neutral relationships between personality and fitness although the evidence cited refers to the contemporary not ancestral environment. They also maintain that the occurrence of a high degree of non-additive genetic variance argues against the selective neutrality of a trait. The evidence on this point is mixed and the non-additive effects seem to vary across measures. Examination of MZ and DZ correlations from a twin study of personality disorder traits, for example, showed modest evidence of non-additivity: these effects were noted in 3 of 18 primary traits and 25 of 69 sub-traits.

The authors argue to the most plausible mechanism for maintaining genetic variation in personality traits is balancing selection. It is difficult to refute their arguments on the significance of this process. It is useful to note, however, that not all psychological mechanisms or structures are necessarily adaptations. Given the complexity of personality and the many different structures and processes involved, this may not be a one mechanism fits all situation.

Although an evolutionary model of personality would potentially shed light on the origins and function of personality structures and processes, it is not clear that the level of analysis adopted by the authors is optimal for this purpose. Like other accounts of the evolution of personality (Buss, 1991, 1997; Figueredo et al., 2005) discussion focuses on the higher-order domains of the five-factor model. However, these domains may be too broad to serve as the basis for formulating hypotheses about the adaptive origins of personality. Although innate mechanisms are complex in design, they are usually specific in function with the different components functioning in an integrated way. Evolutionary psychologists argue that the mental apparatus comprises a relatively large number of these domain specific mechanisms (Simpson, Carruthers, Laurence, & Stich, 2005). It is not clear that the secondary domains of the five-factor model have this specificity. Instead, each domain is complex not just in the sense that any psychological adaptation such as mate selection is complex, but also in the sense that they are multidimensional, each consisting of multiple functionally diverse behaviours and potential adaptive mechanisms. Neuroticism, for example, encompasses anxiety and stress management, dependency and submissiveness, impulsivity and impulse control, and so on.

A more suitable level of analysis would be the primary traits (or facet traits) that form the secondary domains. As the authors note, behavioural genetic research reveals that many primary traits are etiologically distinct entities, each being associated with substantial genetic variance specific to that trait (Jang et al., 1998; Livesley et al., 1998). The genetic architecture to personality appears to be complex and highly specific and primary traits appear to be the fundamental building blocks. These studies also furnish evidence of substantial pleiotropic influences raising the possibility that secondary domains like neuroticism are merely the downstream consequences of pleiotropy. Under these circumstances the search for adaptive mechanisms associated with personality traits and analyses of reaction ranges and “personality signatures” are likely to be more productive if focused on more specific constructs.

Personality Theory Evolves: Breeding Genetics and Cognitive Science

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Abstract

Penke et al.'s (this issue) article makes an important contribution to personality theory, with ramifications beyond genetic studies. It may significantly enhance prediction of behavioral expressions of personality traits from a psychobiological standpoint. Some theoretical challenges remain, including the complex nature of both traits and environmental modulators. The evolutionary genetic model may usefully complement the cognitive-adaptive personality theory developed by Matthews.

This is an important article that should be read by the whole community of personality psychologists, and not just geneticists. Penke et al. (this issue) offer innovative strategies for linking genetic models directly to behavioral expressions of traits. In this commentary, I will focus on the strengths of the authors' approach, some challenging issues, and its convergence with my own cognitive-adaptive model of personality, a theory based on cognitive science rather than genetics (Matthews, in press).

The foundation for contemporary personality trait theory is the evidence that traits predict consequential outcomes (Ozer & Benet-Martinez, 2006). Complementary evidence comes from controlled laboratory studies on the behavioral expressions of traits (Matthews, Deary & Whiteman, 2003). To date, psychobiological models have proved frustratingly limited in their abilities to predict individual differences in behavior to any degree of precision (Matthews & Gilliland, 1999). Much remains to be done to develop the Penke et al. model to the point that it makes detailed predictions of behavior. However, it may be uniquely promising for the following reasons:

Focus on individual differences. Penke et al. rightly indicate both the neglect of systematic individual differences in personality within current evolutionary psychology, and the

limitations of traditional behavior genetic studies. It is encouraging that genetic models have advanced to the point that differing evolutionary explanations for personality variation can be tested against empirical data – this approach has legs.

Solving the isomorphism problem. Zuckerman (1991) pointed out that traits do not map isomorphically onto individual brain systems; instead, traits appears as higher-order emergent properties of multiple systems. The 'watershed' metaphor offers a principled account of why this should be so.

Traits as biosocial constructs. Penke et al. correctly emphasize individual differences in social problem-solving strategies as a key basis for traits. Handling social threats provides adaptive challenges that are much different to those of the spiders, snakes and saber-tooth tigers that provide the prototypical threats in many psychobiological accounts of anxiety (Matthews, 2004). The complexities of handling the subtle challenges of social competition – often in parallel with cooperation, as in sibling rivalry – require more attention.

The evolutionary genetic model has much promise, but there are some potential obstacles to further development of the theory.

Imaging over-enthusiasm. The identification of narrowly defined 'endophenotypes' potentially provides the essential link between polymorphisms and specific, measurable behaviors. However, linking specific polymorphisms to individual differences in brain activation patterns is of limited explanatory power; most studies fail to demonstrate any functional significance to brain activation. Coupled with the somewhat elusive nature of the molecular genetics of personality (e.g., Munafo et al., 2003), modern brain-imaging studies may recapitulate the limitations of traditional psychophysiology as a means for identifying mediating mechanisms that directly govern behavior (see Matthews & Gilliland, 1999). Brain-imaging is invaluable for discriminating component processes, but behavioral studies are requisite for tracing the adaptive implications, if any, of the process concerned.

The perennial problem of the environment. Making something of the 'individual reaction norm' concept requires specification of the environmental factors that control gene expression. Interactionism is the dominant framework for contemporary personality research, but there is a consensus on the difficulties of coding the key environmental modulators of personality. I appreciate the argument is illustrative, but the authors' example of 'environmental stress' is a case in point. There are multitude of environmental stressors that provoke a variety of behavioral responses which are often moderated by

cognitions and context (Matthews, Davies, Westerman, & Stammers, 2000). Interaction of anxiety and stress factors depends critically on the person's appraisals of the stressor, blurring the necessary distinction between the individual and the environment.

The distributed nature of personality. The problem in equating traits with individual reaction norms is that the major traits pervade so many distinct adaptive processes. Neuroticism can be readily related to selective attention, executive processing, metacognition, emotion expression, compensatory effort, as well as to simple emotionality (e.g., Eysenck, Derakshan, Santos, & Calvo, in press). We can generate (possibly large) sets of reaction norms to describe the trait, but the coherence and unity of the trait may be lost in the process. However – similar to Mischel's behavioral signatures – empirical investigation of reaction norms may be a useful descriptive strategy.

Genetics and the cognitive-adaptive theory of personality. I was struck by the authors' identification of balancing-selection mechanisms as pivotal for understanding personality. Their analysis converges closely with the cognitive-adaptive theory of personality (Matthews, 1999, 2000, in press; Matthews & Zeidner, 2004). In brief, the theory proposes that traits correspond to adaptive specializations to some of the more marginal environments that are universal to human societies; e.g., extraversion corresponds to social overload, introversion to underload. Each person (consciously or not) must develop a strategy for handling social threat. High neurotic persons favor anticipation (requiring worry) and avoidance, whereas low neurotics delay response until the threat may be more directly confronted.

Similar to Penke et al.'s model, cognitive-adaptive theory assumes traits confer adaptive gains and costs within specific environments, but are adaptively neutral overall. Cognitive-adaptive theory also states that traits are built on a platform of genetically-influenced basic components of the neural and cognitive architectures, which is modified developmentally by sociocultural learning and autonomous, self-directed shaping of personality. Penke et al.'s theory may add powerfully to understanding the role of genetic antecedents.

Conversely, cognitive-adaptive theory may help to tackle some of the issues facing the evolutionary genetic model. The theory places acquired skills at the forefront of adaptation (cf., Feltovich, Prietula, & Ericsson 2006); skill acquisition is biased but not directly determined by heritable component processes (corresponding to endophenotypes). The theory also explicitly conceptualizes traits as distributed across multiple mechanisms and processes, understood at different levels of abstraction from neural processes (cf., the classical theory of cognitive science: Matthews, 2000). The trait gains unity not from any

specific process but from the common functionality of multiple processes in supporting a specific adaptive strategy. It is critical to explore trait consequences across a range of environments to determine its adaptive significance; perhaps evolutionary personality theory needs a little less Mendel and a little more Darwin.

Do We Know Enough to Infer the Evolutionary Origins of Individual Differences?

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Abstract

Psychologists do not yet understand the role of non-additive genetic influences on personality traits or the number of QTLs for individual traits. Traits vary in their desirability in mates and in their assortative mating. Thus, it is premature to conclude that individual differences in all or any personality traits have evolved by balancing selection.

From my sporadic reading of the literature on the evolutionary psychology of personality traits, the target article appears to represent a notable advance in sophistication. It incorporates new thinking on a number of evolutionary principles and makes an effort to compare rival hypotheses about the origins of individual differences using quantitative estimates of relevant parameters (such as the number of new mutations per individual). I was struck, however, by the frank admission that one of the classical inferences about the relation between fitness and additive genetic variance had been wrong, and the error remained "unnoticed for half a century". There is a moral here, I think: These issues are extremely complex, and it is likely to be some time before we can be fully confident that we understand what is really going on.

The article compares three models of the origins of individual differences, and attempts to rule out two of them—selective neutrality and mutation-selection balance—with regard to personality traits. I will focus on the mutation-selection balance principle, which the authors believe is applicable to intelligence, but not to personality traits. If we assume that their

reasoning is correct, then the conclusion hinges on the factual accuracy of the claims that personality traits fail to show "high additive genetic variation, an elusive molecular genetic basis, condition-dependence, inbreeding and outbreeding effects, strong mate preferences, and assortative mating". These are empirical assertions, and several of them are questionable.

In behavior genetic studies, it is customary to compare models that include additive and non-additive genetic effects and shared and non-shared environmental effects. There is consistent evidence that shared environmental effects are negligible, but a good deal of variation in whether non-additive variance is included in the chosen model. For example, twin studies of the Revised NEO Personality Inventory (NEO-PI-R; Costa & McCrae, 1992) in Canada and Japan concluded that all factors and facets could be suitably described by an additive model (Yamagata et al., 2006). In contrast, Keller, Coventry, Heath, and Martin (2005), using a twin-plus-sibling design, argued that non-additive effects were pervasive in personality measures. Additional evidence for non-additive effects comes from a study of extended family members in Sardinia (Pilia et al., 2006). In that study, broad heritabilities (which include non-additive effects) were much closer in magnitude to the heritabilities seen in twin studies than were narrow heritabilities (additive effects only). As Keller and colleagues point out, the accurate estimation of non-additive effects is difficult, because additive and non-additive effects are strongly inversely related, introducing problems akin to multicolinearity in regression. The data seem to show that there are non-additive effects for some personality traits, but whether the additive effects should be characterized as "large" or "medium" (see Table 1 in the target article) is unclear.

No one who has followed the field would dispute that, to date, the molecular genetic basis of traits has been elusive. After a promising start (Benjamin et al., 1996), attempts to link the D4 domapine receptor gene to personality stalled in a series of failures to replicate (Gebhardt et al., 2000; Vandenbergh, Zonderman, Wang, Uhl, & Costa, 1997). Meta-analyses of the literature on the 5HTTLPR seretonin transporter gene polymorphism (Schinka, Busch, & Robichaux-Keene, 2004) have reached only ambiguous conclusions, with some but not all measures of Neuroticism showing associations.

These studies examined candidate genes, and what may have eluded researchers was perhaps only the right candidates. A more comprehensive approach seeks replicable findings from a whole genome scan; such studies are currently underway (e.g., Costa et al., in press), but have not yet reported findings. It thus remains to be seen whether the number of quantitative trait loci (QTLs) for personality traits is large or small.

Are there strong mate preferences for personality traits? Buss and Barnes (1986) gave respondents a list of 76 characteristics they sought in a mate, including *kind, intelligent, church-goer, good cook, likes children, wealthy,* and *healthy.* Personality traits like *considerate, honest, interesting to talk to,* and *affectionate* were among the top ten desiderata; *early riser, tall,* and *wealthy* were not considered desirable. It is, of course, possible that people's true preferences differ from what they claim: It is socially undesirable to admit to seeking wealth in a mate. Still, the available evidence suggests that people put a high value on personality traits.

Assortative mating is more complex than the authors appear to realize. There is a widespread perception that assortment for personality traits is negligible (about .10) whereas that for intelligence is notably higher (about .40; see Plomin, 1999). Most studies have involved Extraversion and Neuroticism, and the .10 value is reasonable for those factors. But higher values (.20-.30) have been reported for Openness and Conscientiousness (McCrae, 1996), and much higher values for traits related to liberalism/conservatism, which is a facet of Openness. One might argue that assortment for liberal attitudes proceeds from social causes that have little to do with evolutionary processes. But one might make that same argument for intelligence: Intelligent people may prefer intelligent mates, not because they are higher in fitness, but because they are more interesting to talk to.

In sum, we do not seem to have sufficient information at present about personality traits to distinguish among the options of mutation-selection balance and balancing selection. Until we have such information, we ought to avoid the assumption that all personality traits share a single mechanism of evolutionary origin. Traits are all roughly equally heritable (e.g., Jang, McCrae, Angleitner, Riemann, & Livesley, 1998) but we have no way of knowing whether they all have similar numbers of QTLs, and we already know that they differ in assortative mating effects. For the time being, it may be wisest to consider evolution one facet at a time.

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What Do We Really Know About Selection On Personality?

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Abstract

An evolutionary genetic approach to personality in animals and humans necessarily assumes a link between personality traits and fitness. Evolutionary personality psychologists have mainly focused on an a priori conception of this link to build up evolutionary scenarios. Although this approach has added to our understanding of the variance of personality traits, it needs to be accompanied by an empirical examination of the link between these traits and fitness. Several tools developed by evolutionary biologists could therefore be useful in evolutionary personality studies.

Evolutionary ecologists have become interested in personality traits only very recently (Réale et al., 2007), and many felt that, despite a shared interest for similar traits, personality psychologists did not have much in common with them. Using fitness as the currency for their study traits, evolutionary ecologists have mainly been interested in the adaptive function of personality and the ecological role of personality variation. Personality psychologists, on the other hand, seemed to have focused mainly on the social desirability of personalities and the social implications of extreme expressions of personality traits. Penke et al.'s (this issue) thorough review suggests that an interesting convergence may be occurring between the two fields (see also Ellis, Jackson, & Boyce, 2006; Nettle, 2006). Such convergence will promote new ways of looking at personality traits for members of both fields, and should improve our understanding of heritable personality variation.

This said, several points raised in this review may be subject to debate, while other aspects important for the evolutionary study of personality traits are missing. The authors are a bit too quick to reject the role of some factors on personality variation. For example, in a human metapopulation system (Harding & McVean, 2004) genetic drift probably plays a more important role than expected, whereas antagonistic pleiotropy is still one of the main explanations for the maintenance of variation in life-history traits (Roff, 2002). Neither of these explanations is totally incompatible with the hypothesis of fluctuating selection,

and both should be examined more thoroughly prior to being rejected. Rather than giving a detailed listing of such points, I will focus on one major aspect that I think deserves more attention: the link between fitness and personality traits is central to an evolutionary genetic approach to personality, but the way the authors propose to examine this link is somewhat vague. In many instances they mention potential relationships between personality or cognitive abilities and fitness, and the importance of the selection regime for the maintenance of genetic variance, but what do we really know about selection on personality? The study of phenotypic selection, an approach that permits us to examine how quantitative traits are shaped by natural or sexual selection, has experienced strong conceptual and methodological developments since the 80s (Lande & Arnold, 1983; Arnold & Wade, 1984; Endler, 1986; Brodie, Moore, & Janzen, 1995; Hersh & Philips, 2004). However, these developments have been ignored by Penke and co-workers. Below, I show how they can help the development of evolutionary personality studies.

The phenotypic selection study involves evaluating direct and indirect selection acting on traits during a single episode of selection. A directional selection differential (S) represents the change in the mean phenotypic value of a trait resulting from both direct and indirect selection pressures, and is measured as the covariance between the standardized trait and relative fitness. A directional selection gradient (β, i.e. partial regression coefficient in a multiple regression) reflects the change in the mean phenotypic value of a trait resulting from direct selection on this trait, while holding the effects of other traits constant (Lande & Arnold, 1983; Arnold & Wade, 1984). Quadratic terms and interactions between traits can be added to the model to estimate the strength of stabilising/disruptive selection acting on each trait, and correlational selection, respectively. These statistics can be combined with information on the genetic variance/covariance matrix (**G**) to predict the evolutionary response of the traits to selection. Penke et al. (this issue) assume that cognitive abilities are directly and invariably related to fitness, and that personality traits should be under weaker fluctuating selection. Their assumptions, however, are based on an *a priori* conception of how selection acts on these traits. Selection differentials and gradients are standardized statistics. They therefore permit us to compare the strength of selection between different traits or for the same trait between years, environmental conditions or populations (Kingsolver et al., 2001). Using this approach it is thus possible to determine whether personality and intelligence are under different selection regimes, or to test for the presence of fluctuating selection in space and time. The authors also discuss the possibility that variance in personality traits is maintained as a by-product of selection on other traits (see also Nettle, 2006), a hypothesis that can be tested with the phenotypic selection approach.

Phenotypic selection has rarely been used in personality studies in animals (but see Réale & Festa-Bianchet, 2003; Dingemanse & Réale, 2005). In humans a few studies have proposed an equivalent approach (Eaves, Martin, Heath, Hewitt, & Neale, 1990; Nettle, 2005), but to my knowledge none have used the full potential of phenotypic selection analysis. Although, in principle, such approach could be applied to humans, its use may be limited by a few constraints that would need to be examined further. Firstly, the low power of selection studies requires large sample sizes to detect significant selection gradients within the range generally observed in wild populations (i.e. several hundred individuals: Hersch & Phillips, 2004; Kingsolver et al., 2004;). This is especially important if one is interested in detecting weak and invariant selection pressures. Sample size does not seem to be a constraint in studies on humans (e.g. Eaves et al., 1990; Nettle, 2005) and therefore should not be limiting. Secondly, estimates of individual fitness have to be chosen carefully. Penke et al. propose the f-factor, a general index of fitness, but never mentioned explicitly how to use this factor. Lifetime reproductive success is generally considered the most appropriate estimate of fitness, although related indices are available (Brommer, Gustafsson, Pietiaïnen, & Merilä, 2004; Coulson et al., 2006). Other fitness components, like survival, fecundity, or the number of sexual partners can be used, but should be considered with caution because they are potentially involved in evolutionary trade-offs (Roff, 2002). Although the use of such fitness components can be informative for someone interested in decomposing the links between personality and fitness, it can provide an incomplete portrait of selection acting on a trait. Evidence for selection on personality traits in humans using indices more remotely related to fitness should be evaluated with these potential drawbacks in mind.

The evolutionary genetic approach proposed by Penke et al. will certainly provide new sources of inspiration for personality psychologists and evolutionary ecologists. This, and other recent papers (e.g. Ellis et al., 2006; Nettle, 2006), should generate testable predictions that could benefit from methods commonly used in evolutionary biology. We may therefore be witnessing the first steps towards a more integrated evolutionary study of personality in humans and animals.

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Personality: Possible Effects of Inbreeding Depression on Sensation Seeking

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Abstract

Penke et al. (this issue) state that there are no studies of inbreeding depression on personality. In this response to their paper, we look at the effect of parents being born in the same geographical region on personality in themselves and in their offspring. Results show that when parents come from the same region, both they and their offspring score lower on sensation seeking than when parents come from different regions. These results may suggest effects of inbreeding depression on personality.

Studies of inbreeding depression on intelligence (Jensen, 1998) show evidence for inbreeding depression, but - as stated by Penke et al. (this issue) - there are no studies of inbreeding depression on personality. However, Camperio Ciani, Capiluppi, Veronese, and Sartori (2007) reported an interesting comparison of personality traits in Italian coast dwellers and Italians from 3 small island groups. Subjects whose families had lived on the islands for at least 20 generations were lower in extraversion and openness to experience. Penke et al. discuss this finding in the context of “environmental niches” for personality traits, but an alternative explanation might also be possible: the islanders might form a genetically more related group (a genetic isolate) whose offspring shows an effect of inbreeding depression.

To test this hypothesis in an alternative dataset, we took personality data collected in Dutch families consisting of parents and their twin offspring. The families take part in longitudinal survey studies. In 1991 and in 1993 the parents were asked if they had been born in the same geographical region (anwers “yes”, “no” and “don’t know”). We formed 2 groups of families: those whose parents were born in the same geographical region and those whose parents were born in different regions. Please note that same or different region can be a rural or non-rural part of The Netherlands, the question was only about

proximity. We then examined if there were personality differences between the two groups. Personality scores were compared between the two groups in the parental and in the offspring generation. We looked at personality traits related to neuroticism, extraversion, and sensation seeking. We hypothesize that if parents were born in the same geographical region, they may genetically be more related than when they come from different areas of the country, and use this test as an indirect way of looking at inbreeding depression (or its opposite “hybrid vigor”).

Participants. This study is part of an ongoing study on personality, health and lifestyle in twin families registered with the Netherlands Twin Register (NTR; Boomsma et al., 2006). Surveys were mailed to twin families every two to three years. For the present study data from the 1991 and 1993 surveys were used. In total, there were 2905 families. There were 1940 families who took part once (in 1991 or 1993) and 965 who took part at both occasions. Average age of the parents was 46.67 years in 1991 and 47.04 in 1993; average age of their offspring was 17.73 years in 1991 and 20.18 in 1993.

Measures. In both surveys parents of the twins were asked if they had been born in the same region. Data from the two surveys were combined into one yes/no measure. The following 10 personality measures were analyzed: Neuroticism, Extraversion, Somatic Anxiety and Test Attitude (ABV; Wilde, 1970); Thrill And Adventure Seeking, Boredom Susceptibility, Disinhibition and Experience Seeking (Feij & Van Zuilen, 1984; Zuckerman, 1971); trait anger and anxiety were measured using the Dutch adaptation of Spielberger’s State-trait Anger Scale (STAS; Spielberger, Jacobs, Russell, & Crane, 1983; van der Ploeg, Defares, & Spielberger, 1982) and State-trait Anxiety Inventory (STAI, Spielberger, Gorsuch, & Lushene, 1970). Personality measures were averaged over occasions if subjects participated more than once.

Data analyses. We first looked at personality differences between parents being born in the same geographical region and parents being born in different geographical regions, separately for fathers and mothers. In the offspring generation, the same comparisons were carried out separately for first and second born twins to avoid dependency of observations. Data analyses were carried out with SPSS. We employed MANOVA to study group differences. The use of MANOVA prevents the inflation of overall type I error that derives from the use of multiple univariate tests on a group of correlated variables. In the offspring generation sex was introduced as a covariate.

Results. For fathers there was a significant effect of same region on two Sensation Seeking Scales, i.e. Boredom Susceptibility, Experience Seeking. In addition an effect was

seen for Test Attitude. For mothers, Experience Seeking and Test Attitude were also significantly different between groups. In mothers, a significant effect was also observed for Thrill And Adventure Seeking, which also is one of the Sensation Seeking Scales, and Somatic Anxiety (see Table 1). Subjects who were born in the same region as their spouse score higher in Test Attitude, which assesses the tendency to give socially desirable replies. Subjects who were born in the same region as their spouse score lower on Sensation Seeking Scales. Mothers who were born in the same region as their partner show lower Somatic Anxiety. The largest effect size was for Experience Seeking.

- insert Table 1 here -

In the offspring generation there was no effect on Test Attitude. However, Experience Seeking, Boredom Susceptibility, Thrill And Adventure Seeking and Somatic Anxiety also reached significance in first and second born twins. The direction of the differences was the same as in the parental generation (see Table 2). Experience Seeking again shows the largest effect size, and it is the trait that shows significant differences in both parents and both twins.

- insert Table 2 here -

The reappearance of personality differences between parents who were born in the same region and parents who were born in different regions in the offspring generation suggests the presence of inbreeding depression in personality. This is especially true for sensation seeking traits. These results agree with those of Camperio Ciani et al. (2007) who found that subjects whose families had lived on islands for at least 20 generations were lower in openness to experience. Alternative explanations are also possible, e.g. sensation seekers tend to move around more, and their children inherit their sensation seeking tendencies.

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A Multitude of *Environments* for a Consilient Darwinian Meta-Theory of Personality: The Environment of Evolutionary Adaptedness, Local Niches, the Ontogenetic Environment, and Situational Contexts

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Abstract

A consilient and complete evolutionary-based theory of personality must explain the adaptive mechanisms that maintain personality variance at four distinct "environmental" levels: (1) the environment of evolutionary adaptedness; (2) the environment as defined by a given local niche; (3) the ontogenetic environment; (4) the situational environment germane to the person-situation debate in personality theory.

I recently completed a project with one of my graduate students (Richard Sejean) wherein we contrasted the decision-making styles of monozygotic and dizygotic twins and found that these possessed a genetic underpinning. The paper by Penke et al. (this issue) (PDM) is *à propos* as it provides us with a parsimonious set of evolutionary mechanisms capable of maintaining genetic variance in decision-making styles. I suppose that the next challenge is to identify the one-to-one "optimal" mapping between a given decision-making style and a particular environment that would yield such heterogeneity in cognitive proclivities. PDM recognize the importance of this point when they state, "The

challenge…is to identify the specific costs and benefits relevant to each personality trait across different environments." Implicit in addressing this difficult problem is providing an operational definition of the term *environment* in the current context, a point to which I turn to next.

One can speak of the *environment* of evolutionary adaptedness that is central to the adaptationist framework. Hence, universal sex differences in sensation seeking and/or risk taking can be construed as sex-specific adaptations shaped by sexual selection. Alternatively, one can talk about the *environment* in the sense of a local niche in which case personality traits that differ recurrently across populations can be interpreted as adaptations to idiosyncratic milieus (as per Camperio Ciani, Capiluppi, Veronese, & Sartori 2007; see also Dall, Houston, & McNamara, 2004). The ontogenetic *environment* is yet a third type of environment that might shape one's personality via an evolutionary-based mechanism. For example, Sulloway (1995, 1996) has proposed the Darwinian Niche Partitioning Hypothesis as a driver of one's personality. Specifically, he argued that one's birth order yields unique challenges for a given child in its quest to maximize the parental investment that it seeks to receive. Specifically, a child seeks to fill an unoccupied niche as a means of securing maximal parental investment. If a firstborn has already occupied the "I am the obedient good boy" niche then his younger male sibling must identify alternate niches to fill out. As one goes down the birth order the number of unfilled niches is fewer, which Sulloway argues drives laterborns' higher scores on openness to experience. Alternatively, in wishing to maintain their privileged position within the sibship, firstborns are much more likely to score high on conscientiousness. Finally, a fourth type of *environment* is the immediate situational one that is central to the person-situation debate in personality research. In this case, one can talk about the malleability of one's personality as a function of situational demands. Personality traits such as self-monitoring or Machiavellianism might be particularly relevant here as they both recognize an individual's ability to adapt to the situation at hand. The malleable nature of one's personality is akin to the inherent plasticity of our immune system. Specifically, the immune system has evolved the species-level adaptation of being adaptable to idiosyncratic challenges faced by any given organism. This is necessary in order for the immune system to maintain a maximal number of degrees of freedom in its ability to mount defenses against as of yet unforeseen and unknowable attacks. Malleable personality traits in a sense are similar in that they recognize that the social environment is the source of a wide range of environmental challenges and as such must allow for situational plasticity. Wilson, Near, and Miller (1996) applied this exact principle in exploring Machiavellianism from an evolutionary perspective as did Saad (2007, chapter 2). Recent

papers by MacDonald (2005) and Michalski and Shackelford (in press) discuss related multi-level taxonomies for understanding the evolutionary forces that can maintain individual variations in personality (see also Bouchard & Loehlin, 2001, for an evolutionary-based behavioral genetic account of personality).

An evolutionary account of personality must explain G x E interactions across all of the relevant multi-layered levels of analyses. This is easier said than done as most scholars including evolutionists oftentimes create rigid binary categories in defining their research approaches, which can lead to epistemological myopia (e.g., adaptationist versus behavioral ecological approaches; domain-specific versus domain-general view of the human mind; human universals versus individual differences). Although most evolutionists recognize the complementarity of these approaches (cf. Laland & Brown, 2002), they seldom conduct research across multiple levels of analyses. This is precisely where I believe the paper by PDM is most insightful namely it posits distinct forms of balancing selection that "target" several layers of a Darwinian meta-theory of personality. For example, PDM propose that sexually antagonistic co-evolution might be a viable mechanism by which sex differences in personality are maintained whilst arguing that environmental heterogeneity and frequency-dependent selection are likely mechanisms for explaining cross-cultural differences in personality types. This ability to map various sources of personality variance to specific evolutionary mechanisms (at the genetic level) is a necessity if we are to create a truly consilient evolutionary-based theory of personality.

The "multi-layered" meanings of *environment* as described here are congruent with Universal Selection Theory (UST; cf. Cziko, 1995, 2000), which recognizes that evolutionary processes operate across a wide range of levels. For example, while most evolutionists study between-organism selection, UST recognizes that Darwinian processes operate within-organisms as well (e.g., Neural Darwinism as per Edelman, 1987; see also Hull, Langman, & Glenn, 2001, for a broad discussion of selection processes). Finally, while I do not wish to rekindle here the individual versus group selection debate, there is evidence to suggest that for some group decision-making tasks, personality heterogeneity of the group members can at times yield superior outcomes (Bowers, Pharmer, & Salas, 2000; Bradley & Hebert, 1997; Mohammed & Angell, 2003). Hence, an intriguing possibility might be that individual differences in personality are maintained in part because they yield superior group decisions and related outcomes (note that group decision-making is a common decisional context for a social species such as ours).

To conclude, one of the most challenging problems for evolutionary personality theorists will be to identify which form of adaptive process drives a given personality variance, a task tackled admirably by PDM.

Insights from Behavioral Syndromes for the Evolutionary Genetics of Personality

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Abstract

Behavioral ecologists have recently begun emphasizing behavioral syndromes, an analog of personality. This new area offers several insights for the evolutionary genetics of human personality. In particular, it suggests that human personality research could benefit from emphasizing: the evolution of reaction norms, correlational selection, indirect genetic effects, G x E correlations, social situation and partner choice, and social networks.

We study behavioral syndromes, an analog of animal personalities (Sih, Bell, & Johnson, 2004; Sih, Bell, Johnson, & Ziemba, 2004). While many studies on animal personalities focus on the Big Five (Gosling, 2001), the emphasis for behavioral syndromes is typically on ecologically-important behavioral tendencies that have a long history of study by behavioral ecologists, e.g., boldness or aggressiveness. We ask if these behavioral tendencies carry over across contexts. If they do, we expect that sometimes, these carryovers might result in suboptimal behavior. For example, is an animal that is more aggressive than others in competitive contests also inappropriately aggressive with mates or offspring? We also ask if different, but intuitively similar tendencies are positively correlated. Are individuals that are more bold with predators also more aggressive with

conspecifics? Studies have shown that behavioral types (BTs) can be heritable (van Oers, de Jong, van Noordwijk, Kempenaers, & Drent, 2005), have neuroendocrine correlates (Koolhaas et al., 1999) and affect fitness (Dingemanse & Reale, 2005). Many fundamental questions, however, remain unanswered. Why do BTs (or personalities) exist? If a tendency to be aggressive spills over to cause inappropriate aggressiveness in some contexts (psychopathologies?), why has this spillover not been eliminated by natural selection? What explains the structure of the BS? Why are boldness and aggressiveness sometimes, but not always correlated? When and why are BTs and BS stable over time?

Answering the above questions requires a better understanding of the evolutionary genetics of behavioral syndromes. We were thus quite excited to read Penke et al.'s (this issue) comprehensive review of the evolutionary genetics of human personalities. We applaud, in particular, the authors' enthusiasm for adopting a G x E, reaction norm view on the genetics of personality. Our commentary will focus on areas of excitement in the study of behavioral syndromes that might also prove insightful for building an integrative, evolutionary theory of personality for humans and other animals.

The first challenge is to find a suitable model that can explain the maintenance of genetic variation in personality. Most of the models considered by the authors examine the maintenance of genetic variation in non-plastic traits. Behavior, however, is by definition, plastic, in that it involves a response to the environment. The most appropriate models should thus be models which consider the maintenance of genetic variation in reaction norms. While the second half of the paper by Penke et al. champions the importance of the reaction norm view, surprisingly, those insights were not applied to the first half of the paper, which reviewed models on the maintenance of genetic variation.

The theoretical literature on the maintenance of genetic variation in reaction norms is small (but see de Jong & Gavrilets, 2000; Zhang 2005, 2006) but the few models suggest that plasticity can produce some counter-intuitive patterns. For example, in standard models of non-plastic traits, environmental variation and balancing selection tend to facilitate the maintenance of genetic variation (Turelli & Barton, 2004). In contrast, depending on specific scenarios modeled, with reaction norms, greater environmental variation can either increase or decrease the maintenance of genetic variation. The logic on why environmental variation can decrease genetic variation appears to be that with greater environmental variation, plastic genotypes are exposed to stronger overall selection across the range of environments. In any case, the study of both human personality and animal

behavioral syndromes could benefit from further development of models on the maintenance of genetic variation in reaction norms.

Another evolutionary process that deserves attention here is correlational selection, where the fitness of one personality trait depends on how it is combined (correlated) with another behavioral trait. Unlike models that examine environmental heterogeneity and balancing selection which typically assume stabilizing selection with different optima in different environments, evolution via correlational selection is explicitly combinatorial. As the authors note, very high openness to experience combined with high IQ might result in exceptional creativity whereas very high openness combined with low IQ might be viewed as a schizotypic personality disorder. In stickleback fish, boldness and aggressiveness are positively correlated in high predation regimes, but uncorrelated in low predation regimes (Bell, 2005). Experimental exposure to actual predation showed that this correlation is generated by a combination of selection and behavioral plasticity (Bell & Sih, unpublished data). A greater emphasis on correlational selection should be crucial for both theoretical and empirical analyses of the evolution of personalities.

Evolutionary theory can also contribute to human personality genetics by providing a theoretical framework for studying the genetics of social interactions. Social interactions introduce an exciting twist to evolutionary genetics, the possibility of important indirect genetic effects, IGEs (Wolf, Brodie, Cheverud, Moore, & Wade, 1998). IGEs occur when an individual's phenotype (e.g., its aggressiveness) depends not just on its genotype but on its social environment (e.g., the aggressiveness of others). Since the behavior of other individuals has a genetic component, the social environment has a genetic component. This, in effect, decouples the standard genotype-phenotype relationship. The behavior of each individual depends not just on its own genotype, but on the genes of all interacting individuals in its social network. IGEs can have major impacts on evolutionary dynamics. To our knowledge, however, the effects of IGEs on the maintenance of genetic variation has not been quantified.

Standard evolutionary models, models of IGEs and game models all start with the assumption that individuals experience available environments and the mix of genotypes in their social environment in proportion to their relative frequency. In fact, individuals often exercise situation choice – habitat choice, social situation choice, and partner choice. If different personalities have a genetic tendency to choose different situations, this produces a G x E correlation. In the context of partner choice, different personalities might occupy different positions in the social network (which could be quantified using social network

metrics). Unlike habitat choice, social situation and partner choice feature the fascinating complication that individuals cannot independently dictate their own social environment. Social structure and each individual's social partners depend also on the interplay of choices by other individuals. Integrating this reality into evolutionary genetic models should also prove insightful.

Using Newer Behavioural Genetic Models and Evolutionary Considerations to Elucidate Personality Dynamics

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Abstract

We expand on the theme of transactions between persons and situations, and genes and environments. Newer models for twin data can handle genotype-environment transaction effects explicitly, and such models can be used to better articulate the origins of variation in personality.

Penke et al. (this issue) are to be commended on a deep and fascinating contribution to the personality literature. As Penke et al. note, newer techniques in modeling twin data offer ways of more explicitly articulating genotype-environment transactions. We agree with Penke et al. that these newer techniques are central to advancing inquiry in personality genetics, and that interpretation of findings generated by these models will be enhanced by evolutionary thinking.

Traditionally, behavior genetic inquiry has focused on twins because twins are plentiful and studying them provides a way of cleanly separating the different impacts of genotypes and environments on human individual differences. In particular, behavior genetic studies of personality traditionally focused on dividing up the variation in personality traits into the

contributions of genetic (most often additive genetic, or A factors), shared or "common" environmental factors (C, those environments that make people the same because they grew up in the same family), and non-shared environmental factors (E, those environments that make people different in spite of growing up in the same family). Such research consistently finds that A is a substantial proportion of the total variance of a trait (often 40-50%), with the rest of the variation attributable to E (Krueger, Johnson, Plomin, & Caspi, in press). As Penke et al. note, these findings are no longer surprising to many, but they continue to be of central importance for at least two reasons. First, they clearly invalidate models of human individual differences that assume that people are "blank slates" – models that have been historically influential in academic psychology (e.g., classical behaviorist accounts of personality). Second, these findings continue to confound both theoretical and empirical inquiry in personality psychology. If genes are so important to personality, why are specific genetic polymorphisms connected with personality so hard to find (Ebstein, 2006)? And if the non-shared environment (E) is so important to personality, what are the key environmental factors involved, and why have these also been so hard to identify (Turkheimer & Waldron, 2000)?

We do not have easy answers to these tough questions, but we do believe that some key directions can be drawn out from Penke et al.'s thoughtful section on "practical implications for behavioural genetics". As Penke et al. note in point no. 3, models for "genotype x environment interaction (GxE) and correlation (r_{GE})" have been developed recently, and they should be used more frequently. Characterizing these models in terms of GxE and r_{GE} is fine as shorthand, but working with these models also leads us to believe that the concepts of GxE and r_{GE} do not do justice to the transactional phenomena that can be articulated with newer approaches to modeling twin data. Recall that classical behavior genetic inquiry in personality consists of parsing the variance in personality into ACE effects. The newer models Penke et al. are citing (e.g., Purcell, 2002) continue to involve decomposing a variable of interest (a target variable) into ACE effects, but these effects can now be expressed as contingent on the level of another variable (a moderator variable). Hence, in these models, a moderator variable with its own ACE effects moderates the ACE effects on a target variable. The resulting problem with the language of GxE and r_{GE} is that both the moderator and target variables have ACE components – neither variable is purely "genetic" nor purely "environmental". It is not just that purely genetic factors interact and correlate with purely environmental factors (GxE and r_{GE}). Rather, both genetic and environmental effects on both target and moderator variables transact continuously. We will use some findings from our own research to illustrate this point.

Krueger, South, Johnson and Iacono (submitted) examined genetic and environmental (ACE) influences on the broad personality traits of Negative Emotionality, Positive Emotionality, and Constraint in adolescents (the “Big Three”traits, higher in the trait hierarchy than the Big Five traits focused on by Penke et al., this issue; Markon, Krueger, & Watson, 2005). Specifically, Krueger et al. (submitted) examined how ACE effects on those traits varied vary as a function of aspects of the parent-adolescent relationship. Both positive (Parental Regard) and negative (Parental Conflict) aspects of the adolescent’s relationship with both parents were partly heritable (South, Krueger, Johnson, & Iacono, submitted), and both moderated the variance components of Positive and Negative Emotionality.

Interestingly, at high levels of Conflict, the shared environment had a notable effect on the variance in adolescents’ personalities. Indeed, for adolescents with levels of Conflict two standard deviations greater than average, the variance in negative emotionality was as attributable to the shared environment (C) as it was to genetic factors (A). This finding fits well with Penke et al’s emphasis on how circumstances the organism encounters should affect the origins of personality variation in a dynamic fashion. It is tempting to frame this finding in the language of GxE: the “environment” of conflict with parents changes the “genetic” effect on negative emotionality. However, the finding does not fit neatly into the GxE framework because (a) the “environment” of conflict is partly heritable, driven in part by genetic characteristics of the adolescent (cf. Rowe, 1994) and (b) it is not just the genetics of negative emotionality that are affected; environmental contributions to negative emotionality also change as a function of conflict.

While this type of transactional modeling is in its infancy, it has exciting applications in studying personality. An evolutionary theory of personality can guide this work by providing hypotheses about circumstances where gene-environment transactions are likely to occur. As Penke et al note, when socio-cultural relations are beyond normal boundaries, the organism needs to adapt to maximize fitness, so these may be circumstances where specific genetic and environmental effects are highlighted. Broadly speaking, evolutionary psychology can guide our thinking about when and where genes and environments matter, and should thereby be able to help us identify the effects of both specific genetic polymorphisms and environmental circumstances on behavior more reliably.

Neurogenetic Mechanisms Underlying Cognition and Temperament

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Abstract

This commentary discusses the target article's sharp distinction between neurogenetic mechanisms underlying cognitive abilities and temperament. Evidence for associations of genetic polymorphisms with both temperament traits and cognitive control functions and for a shared or at least overlapping neuroanatomy and neuromodulation of cognitive control and of temperament traits may imply that we should consider the existence of cognitive reaction norms.

Penke et al. (this issue) (PDM) must be applauded for their thoughtful and stimulating review of the evolutionary genetics of personality. Their model of the genetic, neurobiological, and environmental influences on cognitive ability and temperament traits provides a broader view on the factors underlying individual differences than many other contemporary models, and the theoretical and practical implications of their integrative approach for personality research go far beyond behaviour genetics.

This commentary relates to PDM's assertion that the distinction between cognitive abilities and temperament reflects different kinds of selection pressures that have shaped distinct genetic architectures underlying cognitive ability and temperament. Indeed, their model may explain why molecular genetic research has been less successful in discovering genetic variation underlying g, while some progress has been made in identifying molecular genetic influences on temperament traits.

However, PDM's sharp distinction between the neurogenetic mechanisms underlying cognitive abilities vs. those mediating temperament differences (see Fig. 3 of the target article) may be challenged if we apprehend cognitive abilities not only as to comprise abilities like reasoning, or verbal, numerical, and figural abilities, but as to also encompass

basic cognitive functions like cognitive control or working memory. Exemplary evidence for this view comes from a twin study by Posthuma, Mulder, Boomsma, and de Geus (2002), who observed a correlation between psychometric IQ, assessed with the WAIS-III, and cognitive control processes, assessed with the Eriksen Flanker task. Interestingly, this correlation was completely mediated by an underlying set of common genes.

In recent years, numerous studies have reported molecular genetic influences on cognitive control or working memory. Intriguingly, accumulating evidence suggests that genetic variation impacting on cognitive functions is also associated with individual differences in temperament traits. In the following, I will shortly review two examples:

1) Variation in the transcriptional control region of the gene encoding the brain-expressed isoform of the serotonin-synthesising enzyme tryptophan hydroxylase (TPH2), TPH2 G-703T, which is associated with amygdala reactivity to emotional faces (Brown et al., 2005; Canli, Congdon, Gutknecht, Constable, & Lesch, 2005), was shown to be associated with the temperament trait Harm Avoidance, with individuals without the -703 T/T genotype exhibiting higher scores in Harm Avoidance (Reuter, Küpper, & Hennig, in press). In another study (Reuter, Ott, Vaitl, & Hennig, in press), this polymorphism was also associated with specific measures of executive control as assessed with the Attention Network Test (ANT, Fan, McCandliss, Sommer, Raz, & Posner, 2001), with individuals without the T/T genotype showing enhanced executive control. Supportive evidence comes from an own study (Strobel et al., submitted), where individuals without the TPH2 -703 T allele showed less reaction time variability and committed fewer errors than T allele carriers in a continuous performance task.

2) A polymorphism in the gene encoding the catecholamine-metabolising enzyme catechol-O methyltransferase, COMT Val158Met, which results in reduced enzyme activity in the presence of the Met allele (Lachman et al., 1996), has been related to higher scores in Harm Avoidance (Enoch, Xu, Ferro, Harris, & Goldman, 2003) and Neuroticism (Eley et al., 2003). On the other hand, the Met variant has been associated with better performance in cognitive tests of prefrontal function including better working memory (Egan et al., 2001; Goldberg et al., 2003) and less perseverative errors in the Wisconsin Card Sorting Test (Egan et al., 2001, Malhotra et al., 2002).

Several further examples could be given for such pleiotropic effects, e.g. for polymorphisms in the genes encoding brain-derived neurotrophic factor or the serotonin transporter. It appears that this evidence provides examples for *antagonistic pleiotropy,* i.e. genetic polymorphisms have a positive effect on one trait and a negative effect on another.

However, as PDM convincingly argue, antagonistic pleiotropy tends to be evolutionary unstable. Rather, the mentioned findings may be viewed as examples for *structural pleiotropy* (at least in a broader sense), i.e. polymorphisms influence neurobiological mechanisms that are shared by different traits. Indeed, the brain circuitry assumed to be involved in cognitive control (e.g. Miller & Cohen, 2001) shows considerable overlap with structures suggested to modulate temperament traits (e.g. Depue & Collins, 1999; Gray & McNaughton, 2000). This brain circuitry comprises prefrontal cortex, amygdala, hippocampus, nucleus accumbens, thalamus, and other structures, with the information flow within this cortico-subcortico-thalamic network being crucially dependent on neuromodulatory influences exerted by dopamine (see Grace, 2000), but also, among others, serotonin (Robbins, 2005). Hence, genetic variation impacting on dopamine function (e.g. via variation in COMT enzyme activity) or serotonin function (e.g. via TPH2-mediated variation in serotonin availability) is likely to influence a number of behaviours associated with the cortico-subcortico-thalamic circuitry, although neuromodulatory influences and the information flow within this network may differ from one situation (being confronted with emotional stimuli) to another (being challenged by demanding cognitive tasks).

How, then, could the evidence for shared or at least overlapping neurogenetic mechanisms underlying both temperament and cognitive control be reconceiled with the model proposed by PDM? Perhaps, we might consider to assume a third category besides – or between – cognitive abilities as fitness components under mutation-selection and temperament traits as reaction norms with environment-contingent fitness consequences being under balancing selection. I would suggest this third category to comprise *cognitive reaction norms*. These cognitive reactions norms may also be under balancing selection, because cognitive control functions – albeit being *cognitive* in nature and being recruited when cognitive ability is challenged – are *reaction norms* in the sense that they are to some degree also situation- or environment-contingent: There are situations, or environments, where the ability to shield working memory representations against distracting information enhances fitness, and there are situations, or environments, where flexible updating of representations and rapid switching of goals or of the means to achieve them is more appropriate.

It remains to be determined how exactly associations of genetic polymorphisms with cognitive functions and temperament are mediated by variation in the same vs. different brain functions. Nevertheless, the assumption of a category of behavioural differences located between and sharing genetic and/or (endo)phenotypic variance with cognitive

ability and temperament could help to resolve the ambiguous nature of temperament traits correlated with general intelligence.

The Relevance of Personality Disorders for an Evolutionary Genetics of Personality

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Abstract

The epidemiology of personality disorders confirms the importance of the evolutionary approach to a better understanding of individual differences in personality traits and adds credibility to the evolutionary genetic model. A full appreciation of the potential of the evolutionary genetic framework requires a critical revision of current measures of personality.

Penke et al. (this issue) address the unsolved question of explaining persistent genetic variation in personality differences, examine data for and against three evolutionary genetic mechanisms (i.e., selective neutrality, mutation-selection balance, and balancing selection), and conclude that balancing selection by environmental heterogeneity seems best at explaining genetic variance in personality traits. The article focuses on personality differences in the normal range and limits the discussion of personality disorders to sketching some hypotheses that could explain their origin. However, a detailed examination of the epidemiology of personality disorders confirms the importance of the evolutionary approach to a better understanding of individual differences in personality traits and adds credibility to the evolutionary genetic model proposed by Penke et al.

The National Comorbidity Survey Replication (NCS-R) study has recently reported data on the prevalence and correlates of DSM-IV personality disorders in the general population of the United States (Lenzenweger, Lane, Loranger, & Kessler, 2007). Two unexpected findings were that personality disorder is a relatively common form of psychopathology

(point prevalence: 9.1%) and that a diagnosis of personality disorder not comorbid with Axis I syndromes has only modest effects on functional impairment. Taken together, these findings cast doubt on the traditional view of personality disorders as dysfunctional and maladaptive extremes of normal personality traits produced by rare genotypes and raise the question if these behavioral phenotypes have been adaptive in some environments or during some periods of human evolution. In other words, we cannot exclude that not only normal personality differences but also personality disorders are the product of a set of varying selection pressures favoring different phenotypes under different environmental conditions (Troisi, 2005).

Epidemiological data on personality disorders also suggest that gender and age configure different socio-environmental niches. The DSM-IV general criteria for a diagnosis of personality disorder require that the “enduring pattern” (as defined in criteria A-C) be “stable and of long duration…” and “…onset can be traced back at least to adolescence or early adulthood” (criterion D). Such a definition reflects the traditional view of personality disorders as persistent, enduring, and stable patterns. However, available data suggest that some personality disorder diagnoses demonstrate only moderate stability and that they can show improvement over time. Cluster B personality disorders (antisocial, borderline, narcissistic and histrionic personality disorders) tend to become less evident or to remit with age (van Alphen, Engelen, Kuin, & Derksen, 2006). In particular, the behavior characteristics of antisocial personality disorder (ASPD) first appear during adolescence and often disappear during the fifth decade, and all large-scale epidemiologic surveys of ASPD confirm that at least 80% of those meeting criteria are men. If ASPD is viewed as a risk-taking behavioral strategy, its improvement with age and higher prevalence among males fit with the pattern one would predict from a life-history theory perspective.

Patterns in risk-taking are related to life-history variables, which include gender, age, marital and parental status, amount and predictability of resources, and rates and sources of mortality. Among patients with ASPD, ages 15-29 are those of most severe manifestation of the disordered personality traits, including impulsivity, aggressiveness, irresponsibility, and sensation-seeking. Among males in the general population, these are the years of highest risk for motorcycle accidents and arrest for assault. From a life-history theory perspective, the common explanation for these clinical and socio-demographic findings lies in the role of risk-taking in reproductive competition, which is typically more intense for young men than for women or older men. During the teens and young adult years, competition for social and economic resources is acute, and one’s fate in the mating market is being determined. For males at younger ages, the optimal strategy is to take

risks to acquire resources for immediate use in reproductive effort, especially when environmental characteristics are uncertain and unpredictable (Hill & Chow, 2002).

In line with this argument, it is not surprising that personality disorders reflecting an internalizing dimension (i.e., mood and anxiety), such as for example dependent personality disorder, tend to be more prevalent among women (Torgersen, Kringlen, & Cramer, 2001). In contexts where infant survival would usually depend on the mother's survival more than the father's, women are expected to have been selected for a greater tendency than men for self-preservation (Campbell, 1999).

Another crucial question addressed by Penke et al. is the validity of current measures for studying personality differences from the perspective of evolutionary genetics. The authors appropriately draw attention to the limits of self-report questionnaires, recommend changes based on the assessment of behavioral reactions to specific fitness-relevant situations, and argue for a wider use of the endophenotype approach. However, they seem satisfied with the Five Factor Model of personality and consider attachment styles as non-genetic personality traits. In effect, attachment research has generally presumed environmental mechanisms explaining individual differences in attachment security without, until recently, testing for possible genetic effects. However, in recent years, several behavioral genetic and molecular genetic studies have been conducted, and there is preliminary evidence for gene-by-environment interactions in the development of attachment styles. Recently, the first study combining molecular genetics with measurement of environmental influences (i.e., mothers' unresolved loss/trauma or frightening behavior) on disorganized attachment has been conducted in children of 14-15 months of age (Van IJzendoorn & Bakermans-Kranenburg, 2006). Results showed that the DRD4 polymorphism (short versus long) and the -521 C/T promoter gene were not associated with disorganized attachment. However, a moderating role of the DRD4 gene was found: Maternal unresolved loss or trauma was associated with infant disorganization, but only in the presence of the DRD4 7-repeat polymorphism. The increase in risk for disorganization in children with the 7-repeat allele exposed to maternal unresolved loss/trauma compared to children without these combined risks was 18.8 fold. The T.7 haplotype showed a similar interaction effect: an elevated risk for infant disorganization in the case of maternal unresolved loss (odds ratio 3.24).

If these preliminary data will be confirmed and expanded, attachment styles could be included among personality profiles amenable to an evolutionary genetic analysis. Such a possibility has been already suggested by Belsky (1999). In contrast with the traditional

perspective of clinical psychology that views insecure attachment patterns as reflecting some kind of personality pathology, Belsky has advanced the hypothesis that, in the ancestral environment, all the patterns of attachment were equally adaptive in terms of promoting reproductive fitness in the ecological niches that gave rise to them. According to his hypothesis, the main evolutionary function of early social experience was to prepare children for the social and physical environments they were likely to inhabit during their lifetimes. Thus, attachment patterns could represent evolved psychological mechanisms that used the quality of parental care received during childhood as a cue for optimizing adult reproductive strategies, as indicated by the strict association of each adult attachment style with different sexual and parental behaviors.

The Need for Interdisciplinary Research in Personality Studies

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Abstract

The target article demonstrates the value of evolutionary genetics for personality research. Apart from a summing-up of concepts, the authors validate their theory with evidence from studies on both human- and animal personality. In this commentary, I want to show the need for inter-disciplinary research to answer questions on personality in psychology and biology.

The target article provides the reader with a very comprehensive review on how both traditional and modern evolutionary genetics may help us understand the maintenance of personality variation. The article gives us elaborate explanations of evolutionary genetical processes in combination with clear predictions for personality. Moreover, apart from a sum-up of concepts, the authors critically evaluate the theories of others, and validate their own with evidence from a wide range of studies. Where the authors were not able to confirm their argument with data from human personality research, they easily shifted to work on non-human animals. This clearly shows the importance of studies across disciplines.

Although a recent discovery of animal personalities was suggested in the target article, several animal psychologists had already started using methods from human personality research in the 1960s. Studies were mainly on primate species (see Buirski, Plutchik, & Kellerman, 1978). Yet, in spite of the obviousness of personality differences within many animal species (Wilson, Clark, Coleman, & Dearstyne, 1994; Gosling & John, 1999), very little work was carried out in evolutionary research because of the fear of being accused of anthropomorphism. And although the use of animals for studying personality is still controversial (Gosling & Vazire, 2002), animal models have now proven to be a useful tool for studying the underlying physiological and genetical mechanisms of personality (e.g. Koolhaas et al., 2001). These, mainly rodent studies, however were all on captive-bred populations and therefore give no insight into the evolutionary processes that shaped these traits (Merilä & Sheldon, 2001).

Gradually the view changed that measured individual differences are only characterised by an adaptive mean flanked by non-adaptive variation, into the idea that variation in itself can also be maintained by natural selection (Wilson, 1998). Moreover, behavioural ecologists who usually studied one trait at a time now realized that traits do not evolve independently, but from an evolutionary compromise to optimize fitness over a range of traits. Therefore, more and more biological studies now try to integrate personality into evolutionary biology (Sih, Bell, & Johnson, 2004; Réale et al., in press). In contrast, psychologists are now trying to integrate evolutionary theory (e.g. Buss, 1991) and evolutionary genetics (presented in the target article) into the present knowledge on human personality. Evolutionary biology thereby has a long standing tradition in interest in fitness consequences, mostly directly measured by the response to selection on life history traits (Stearns, 1997).

Two different approaches for studying trait evolution can thereby be recognised, phenotypic and genetic (Lessells, 1999). In a phenotypic approach questions about the adaptive value of a trait are asked and the genetic approach considers the effect of selection, but mainly how selection will affect gene frequencies (see e.g. Via & Lande, 1985; De Jong & Van Noordwijk, 1992) and the genetic structure of traits (see e.g. Roff, 1997). The authors show the value of the second approach for understanding evolutionary processes in humans and the similarity with animals. However, as the authors state: “the central question for an evolutionary personality psychology is: how do psychological differences relate to fitness (the f-factor in Miller, 2000c)”. Although in humans, personality has been shown to influence the success of an individual, by affecting social relationships, school- and career success, and health promotion and maintenance (e.g. Caspi, Roberts,

& Shiner, 2005), the phenotypic approach has still been neglected. What is lacking, are studies that link variation in individual success due to phenotypic variation in personality with life history characteristics; aiming to explain genetic changes over generations. Since the target article shows that similar selection profiles are present for humans and non-human animals, similar approaches in measuring fitness should be feasible. Yet, only one study has looked at fitness aspects of human personality traits by comparing reproductive fitness among different groups (Eaves, Martin, Heath, & Hewitt, 1990).

One example where direct measurements of selection pressures are needed is presented in the studies of Ciani and colleagues (Camperio Ciani, Capiluppi, Veronese, & Sartori, 2007). Italian coast-dwellers were compared to people living on three small islands off the coast of Italy. Personality differences were studied and population differences were ascribed to genetic differences due to dissimilar fitness payoffs. However, populations may differ from each other because of many reasons (Roff, 1997). It is therefore even more likely that the differences are not caused by genetic change, but are due to e.g. differential dispersal patterns, founder effects and genetic drift.

I am conscious of the difficulties in measuring selection in a direct way in studies on human personalities, although I believe that it is mainly disbelief that prevents us doing it. Twin studies could be immensely valuable in this, but they have some methodological limitations, especially since natural experiments do not permit full experimental control. Also the alternative approach suggested in the target article (the use of endophenotypes) may have a serious drawback: underlying mechanisms like hormonal mechanisms may on hand be used to assess personality differences, on the other hand they also present a context dependent expression of personality (see e.g. Carere & Van Oers, 2004).

Animal studies could, however, be helpful in answering questions on selection pressures. They are able to measure the actual consequences of personality differences on life history characters such as reproduction and survival by manipulating the social and/or non-social environment. Animal studies may thereby profit from the substantial knowledge on personality development and the molecular genetic background of human studies. We need, however, to evaluate current methods how personality is measured, validate similarities between humans and non-human animal personalities and compare relevant selection processes. Promising starting points are a common molecular genetic basis (Ebstein et al., 1996), underlying physiological mechanisms.

In conclusion, many proximate and ultimate factors underlying personality differences remain to be tested in both humans and non-human animals. The two distinct areas

(biology and psychology) have built up their own specific knowledge, but the target article shows that these findings can successfully be combined in building a shared theory. Interdisciplinary work combining these efforts in cooperative projects would thereby enhance this process and will allow us to measure micro-evolutionary processes that play a role in shaping personality variation in humans and other animals.

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Authors' response: Evolution, genes, and interdisciplinary personality research

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Abstract

Most commentaries welcomed an evolutionary genetic approach to personality, but several raised concerns about our integrative model. In response, we clarify the scientific status of evolutionary genetic theory and explain the plausibility and value of our evolutionary genetic model of personality, despite some shortcomings with the currently available theories and data. We also have a closer look at mate choice for personality traits, point to promising ways to assess evolutionarily relevant environmental factors, and defend higher-order personality domains and the g factor as the best units for evolutionary genetic analyses. Finally, we discuss which extensions of and alternatives to our model appear most fruitful, and end with a call for more interdisciplinary personality research grounded in evolutionary theory.

We were gratefully impressed to learn that our target article received 22 commentaries, coming from disciplines as diverse as traditional personality psychology (**Funder; Matthews; McCrae**), molecular behaviour genetics (**Bates; Lee; Strobel**), quantitative behaviour genetics (**Jang; Johnson; Livesley; South & Krueger; Rebollo & Boomsma**), evolutionary behavioural ecology (**Dingemanse; Réale; Sih & Bell; van Oers**) and

evolutionary psychology (**Campbell; Euler; Figueredo & Gladden; Gangestad; Keller; Saad; Troisi**). This shows the scientific community's high level of interest in understanding heritable personality differences within an evolutionary framework. The volume of commentary is also a testament to the interdisciplinary challenge such an endeavour entails. We would like to thank all commentators for their thoughtful remarks and constructive criticism.

The overarching goal of our article was to provide a theoretical introduction to evolutionary genetics for personality psychologists. Therefore, we found it especially pleasing that most commentators appeared open to an evolutionary genetic approach to personality, or even applauded it. We take this as an affirmation that our most central message – that personality psychology can benefit from an evolutionary approach grounded in evolutionary genetics – is already widely acceptable, if not fully accepted.

Our second major goal was to try to infer the mechanisms that maintain genetic variation in personality differences, given the predictions from different evolutionary genetic models, and the phenotypic and genetic evidence available from personality psychology. Most commentaries focused on specific assumptions, conclusions, or details of our resulting evolutionary genetic model of personality. As **Keller** states, such healthy discussion is crucial in strengthening the relatively young scientific movement of evolutionary behavioural genetics. Of course, our evolutionary model of personality is only one possible reading of the current state of evolutionary genetic theory and the empirical research on human personality. It should be regarded as an initial working model that should be challenged, refined, and extended.

In this response to commentaries, we will first reply to objections to the theoretical reasoning and use of empirical evidence in our target article, and then discuss more general issues – the optimal levels at which we should study the evolutionary genetics of personality, how our model should be extended in the future, and which alternatives could be explored further. Because so many researchers from diverse backgrounds made comments that were often quite specific, space limitations did not permit us to reply in detail to every point. However, we tried to address the key recurring themes in this rejoinder, and hope that such debate leads multidisciplinary research on the evolutionary genetics of personality to flourish in the future.

Evolutionary genetics as a theoretical framework for personality psychology

Funder and **McCrae** applauded our approach as being a healthy departure from the early days of "evolutionary" accounts of personality that could not be refuted by empirical evidence. In contrast, **Bates** criticized our attempt as using "armchair" evolutionary theorizing instead of hard empirical "field work" to settle the evolutionary history of traits. We think this

"data-first" bias, shared by **Bates** and many other personality researchers, is an understandable reaction to the peculiar history of personality psychology, but is now inhibiting progressive research. Before the trait approach integrated factor-analytic, cross-cultural, and behaviour genetic studies of personality structure, personality psychology was a mess – a hodgepodge of Freud, Rogers, Maslow, and other "classic figures" who were long on theory and short on data. Frustration with this history (in which theory has more often retarded research than advanced it) has inoculated many personality psychologists against anything that sounds like theory. Here, we simply point out that evolutionary genetic theory has quite a different status than Maslow's hierarchy of needs, or any other traditional "personality theory". Evolutionary genetic theory is the dominant formal way that biologists use to think about the effects of selection, mutation, drift, and migration on the genetic structures of traits and populations. It is the mathematical heart of biology, and is rooted in 140 years of progressive research. Well-established evolutionary genetic theories do not share the same limitations of traditional "personality theories". In any case, we repeatedly descended from theory's armchair to compare evolutionary genetic predictions against the current state of empirical knowledge on human personality differences.

Can we already tell something useful about the evolutionary genetics of personality?

To infer evolutionary histories and selective regimes from personality data is indeed a big step, dependent on the quality of both available data and theoretical models. **McCrae** asks if we really know enough to take this step, and **Keller** reminds us to be careful and critical before claiming firm conclusions. Evolutionary genetics, while well-established and intimately intertwined with quantitative genetics in evolutionary biology (**Gangestad**), is a rather new area for most psychologists and behaviour geneticists, who have only just begun to recognize its potential. We would hate to derail such a development through premature conclusions. It is also true that most theoretical models still provide at best ordinal predictions about trait characteristics for realistic evolutionary conditions (**Euler**), and that the relevant empirical data are still incomplete, though maybe not as indecisive as suggested by **Bates**, **McCrae**, and **Keller** (a point to which we will return below). Therefore, the model we proposed is not the only possible one, and it should not be understood as conclusive (see p. 31). However, as the Table 1 in our target article shows, even though the theoretical predictions for individual characteristics of traits shaped by certain evolutionary mechanisms are sometimes vague, the *pattern* of predictions that emerges across various characteristics clearly discriminates between them. Similarly, even though the quality of available empirical evidence for the individual characteristics varies widely, it was the overall pattern of data that struck us and led us to propose the model that general intelligence is under mutation-selection balance, whereas personality traits are under balancing selection.

Before we discuss how decisive the different predictions and lines of evidence really are, we would like to address the usefulness of an "inconclusive" evolutionary genetic personality model. After all, **Keller** called for an exceptionally high standard of evidence at the current stage. We agree that it is likely too early to draw a *conclusive* model, but we see the merits of proposing a sufficiently *plausible* model to help generate new hypotheses, guide empirical research, and inform theories about personality in general (see **Funder** and **Matthews**). The important point is that a plausible model should be explicitly labelled as such and should not blind researchers to alternatives. Nor should it constrain empirical endeavours, which could lead to scientific myopia. Contrary to **Bates**' reading of our target article, we did not call for a theory-driven moratorium on any particular kind of research, even including molecular genetic studies on the genetic bases of general intelligence (*g*). Instead, we explicitly stated that such studies should be done to test the predictions of our model, though they might benefit from being more theoretically informed.

Can we already make inferences from genetic architectures?

Keller questioned our use of genetic architecture information to infer mechanisms of genetic variance maintenance. This criticism has a theoretical and an empirical aspect that are somewhat mixed up in his commentary. On theoretical grounds, we have to agree with **Keller** and also with **Figueredo & Gladden** that it is hard at the moment to discriminate between mutation-selection balance and balancing selection based on the relative contribution of non-additive genetic variance (V_{NA}) to the total genetic variance of a trait (i.e., the coefficient D_{α}). We acknowledged the inconclusiveness of the current literature on page 12, but were less explicit about it later on (especially in Table 1, where we simply stated the prediction we regard as most likely). As **Keller** rightly stated, the prediction that the proportion of V_{NA} will be medium for traits under mutation-selection balance and large for traits under balancing selection might be considered as the weakest in Table 1.

However, we do not follow **Keller**'s sudden dismissal of the prediction that V_{NA} will be higher in traits under selection (including mutation-selection balance and balancing selection) than in neutral traits. The argument here is that selection tends to deplete additive genetic variance (V_A), while V_{NA} is largely robust against selection. (On a side note, **Lee** is right that this is an extrapolation from Fisher's fundamental theorem, but a widespread one that is correct under many conditions, e.g. Roff, 1997.) Nor does **Keller** provide a theoretical counter-argument. Instead, he points to the rather independent issue of *empirical* difficulties with the establishment of V_{NA} estimates, a topic on which we totally agree. In humans, most inferences about genetic architectures come from twin studies (e.g. **Livesley**), where the traditional design confounds V_A and V_{NA}, and V_{NA} can only be estimated when shared

environmental influences are neglected. In line with Keller and Coventry (2005), we think that studies with large extended twin-family designs would provide the best solution.

Furthermore, **Keller** noted that the unknown scale properties of most personality questionnaires and ability tests render rather uncertain even the existing estimates of genetic variance components from more powerful designs. As support, he cited a recent study by Lykken (2006) in which a scale transformation eliminated the V_{NA} component of skin conductance level, a psychophysiological measure of arousal. However, Lykken (2006) argues that this correction actually served as a statistical control for all kinds of confounding factors beyond arousal that influence skin conductance (e.g. individual differences in the density and reactivity of sweat glands). In such cases where the scale transformation decreases the complexity of the measured construct, a reduction in V_{NA} is what should be expected. This does not undermine the general validity of the untransformed score or the scale of the applied measure; it just shows that the untransformed score reflects a construct that is influenced by several interacting heritable components (Lykken, 2006). In our model, such a transformation would correspond to a statistical control of all but one of the interacting endophenotypic personality mechanisms. If a transformation like that becomes ever possible for personality traits, we would also predict a decline of V_{NA}. We agree with **Keller** (see also **Bates**) that the development of new personality measures with improved scale properties (esp. ratio scales, see p. 30) is highly desirable, but we put more trust in the V_{NA} estimates from extended twin-family designs than **Keller** does. While these results might not help us very much to discriminate between different forms of selection on personality differences (mutation-selection balance vs. balancing selection), they do suggest that selective neutrality of personality, as favoured by **Campbell**, is unlikely.

While it is hardly possible to distinguish between mutation-selection balance and balancing selection based on just V_{NA} estimates, data on inbreeding depression can be more decisive. This is because polygenetic traits under mutation-selection balance should always show inbreeding depression, while only traits under balancing selection through overdominance will (**Keller**), and overdominance is actually rare and evolutionarily unstable. In this case, the problem is on the empirical side: Experimental inbreeding studies are only possible in non-human animals, and strong natural experiments (e.g. children from cousin marriages) are rare. Fortunately, this kind of inbreeding data exists for intelligence (supporting mutation-selection balance), but is lacking completely for personality traits. In a noteworthy first attempt to fill this gap, **Rebollo & Boomsma** reinterpreted Camperio Ciani et al.'s (2007) study, and also reported their own data, on personality differences between parents and their children who mated with a spouse from a geographically close or distant region. Both studies together suggest that those who mate within the same regions (which may reflect stronger inbreeding effects) have children who are lower on sensation seeking

(esp. excitement seeking) and openness to experience, while results are unclear for extraversion and there was no effect for neuroticism, agreeableness, conscientiousness, anxiety, or anger. The problem with these results is that they are very indirect and allow for various alternative interpretations. It is especially striking that effects were found exclusively for traits (i.e. sensation seeking and openness to experience) that can be directly associated with migration tendencies and active niche selection. This is most obvious in the worldwide distribution of DRD4 polymorphisms, which suggests that carriers of the allele that has been associated with high sensation seeking are more likely to migrate (Chen, Burton, Greenberger & Dmitrieva, 1999). It is also striking that **Rebollo & Boomsma** found the sensation seeking difference already in the parent generation, even though we know nothing about the geographical mating habits of their parents. As these authors themselves state, migration might be a plausible alternative explanation for these particular results. What we need next are studies of inbreeding effects on personality traits with stronger designs (some suggestions are given by Mingroni, 2004).

Similar conclusions can be drawn for the other aspects of genetic architecture we discussed: while the theoretical models are specific enough to make predictions that distinguish at least one of the major evolutionary mechanisms for the maintenance of genetic variance from the other two, most empirical evidence on the number of genetic loci, the number of polymorphic loci, and the average effect size of loci is still rather indirect. Again, the overall pattern of results allows us to evaluate which mechanism is the most plausible for a given trait, but better data is needed to substantiate these conclusions.

Is mate choice similar for intelligence and personality traits?

On the phenotypic level, evolutionary genetic theory suggests that traits under mutation-selection balance, but not traits under balancing selection or selectively neutral traits, should be sexually attractive in a general, species-typical way. The logic here is that choosing sexual partners based on reliable indicators of low mutation load will endow potential offspring with “good genes”. In our target article, we argued that studies on human mate choice support general mate preferences and assortative mating for intelligence, but not for personality traits. **McCrae** doubts this claim. He remarks that studies on self-reported mate preferences often find strong preferences for personal attributes such as “honest”, “considerate”, and “affectionate”, which can be ascribed to the agreeableness domain. However, aside from the problem that self-reported preferences often do not reflect actual mate choices (Penke, Todd, Lenton & Fasolo, in press), it is important to distinguish between sexual attraction per se and pragmatic preferences for long-term mates. Long-term relationships are, ideally, cooperative relationships, so people prefer honest and trustworthy partners for long-term mating relationships, just as in other social relationships (Cottrell,

Neuberg & Li, 2007). The likely reason for this, however, is not sexual attraction per se, but the pragmatic avoidance of exploitation, distress, inconvenience, and inefficient coordination (called “relationship load” by Buss, 2006). This becomes obvious in studies where preferences are assessed across different mating contexts and relationship durations (e.g. Kenrick, Groth, Trost & Sadalla, 1993). These studies show that the preference for agreeableness-related attributes vanishes when a mate is chosen for a sexual affair or a one-night-stand, where not much cooperation is necessary. Furthermore, it is unclear whether the long-term preference for warmth and trustworthiness really reflects the ideal of an agreeable mate personality (i.e., a trait of an individual), or the ideal of a secure attachment relationship (i.e., a dyadic trait) (Penke et al., in press). At least from an evolutionary theoretical perspective, people should seek a long-term partner who is faithful and supportive within the context of the relationship, but people should be less concerned their partner’s behaviour towards, for example, alternative mates, rivals, or out-group members. Exceptions might be traits like benevolence, generosity, heroic virtues, and magnanimity. These agreeable characteristics seem to be sexually attractive in short-term and long-term mates, but apparently because they are reliable indicators of good condition and low mutation load (Miller, 2007; Griskevicius et al., in press). However, the important point here is that high agreeableness per se is not sexually attractive, but some specific forms of agreeableness are generally attractive if they can only be displayed by individuals in good condition. Similarly, only people with high intelligence will be able to convert a high openness to experience into sexually attractive degrees of creativity (Miller, 2000a; Haselton & Miller, 2006). These personality traits are not always sexually attractive in themselves, but can be attractive under certain circumstances, when they advertise good condition and genetic fitness.

McCrae also noted that some degree of assortative mating has sometimes been shown for conscientiousness and openness to experience, but other studies (e.g. Watson et al., 2004) failed to show assortative mating on these traits. We are not aware of a meta-analysis of the large human assortative mating literature, but the general picture is that assortative mating for intelligence is a well-established phenomenon, while findings are rather weak and inconsistent for individual personality traits.

Finally, **McCrae** mentions that assortative mating can result from social homogamy (i.e., choosing a mate from within one’s self-selected social environment, such as college, job, or neighborhood), not just from direct assortment on perceived traits within competitive mating markets. More sophisticated research designs are able to disentangle these two alternatives, and they reveal that direct preferences exist independent of social homogamy, especially for intelligence (e.g. Reynolds et al., 2000; Watson et al., 2004).

Overall, we think it is fair to say that intelligence is very often directly preferred in mate choice, while the evidence does not support such a general conclusion for personality traits.

Is personality evolutionarily relevant at all?

The most important kind of evidence to distinguish between selective neutrality and any selection-based account for heritable personality differences (including mutation-selection balance and balancing selection) is the empirical link between personality and fitness. Only if personality differences have behavioural consequences that influence fitness, can we posit that some form of selection acts directly on personality. Fitness is ideally operationalized as the relative long-term (multi-generational) reproductive success of genotypes in populations, but phenotypic selection studies have established more practical operationalizations of fitness, such as measured reproductive success over a single lifespan or even shorter periods such as breeding seasons (**Réale**). Since the necessary data is not hard to gather for human personality, it is both surprising and unfortunate that human phenotypic selection studies are extremely rare. More of these studies are desperately needed to inform an evolutionary genetic approach to personality (**Dingemanse**; **Réale**; **van Oers**).

But does this mean that we have to fall back to the most "parsimonious" baseline model of selective neutrality, as suggested by **Campbell**? We don't think so. As calculated by Keller and Miller (2006), the correlation between a truly neutral trait and fitness must not be greater than ±.0055 (i.e., the square root of the maximal .003% fitness difference under which genetic drift is a more important factor than selection, given typical ancestral human population sizes). This effect size is greatly exceeded in the few studies that directly link personality differences to general reproductive fitness in humans (e.g. Eaves et al., 1990) and other animals (see Dingemanse & Réale, 2004), and in the much more numerous studies that link personality differences to specific components of human fitness (such as survival, social status, mating success, and reproductive strategies; see our target article for references). Even if it turned out that genetic drift had been somewhat stronger throughout our evolutionary history than assumed in Keller and Miller's calculation (**Réale**), which would allow somewhat greater effect sizes for neutral traits, and even though the effect sizes for single fitness components should be interpreted with caution because of evolutionary trade-offs (**Réale**), it seems highly unlikely that all of the well-documented behavioural consequences of personality differences are invisible to selection.

Finally, note that the selective non-neutrality of personality differences contradicts not only Tooby and Cosmides' (1990) neutrality account for the maintenance of genetic variance in personality, but also their pathogen-defence hypothesis (**Campbell**, **Livesley**). This hypothesis assumes that the *behavioural* consequences of personality differences are so invisible to selection that their genetic foundations can vary freely, such that the organism's

proteome is more distinctive, unpredictable, and harder for pathogens to exploit. Even if all personality-related polymorphisms (such as DRD4 or 5-HTTLPR) had pleiotropic effects at the level of organismic biochemistry that are relevant to anti-pathogen defence, any such anti-pathogen effects would need to be larger than the behavioural fitness payoffs of personality differences, in order for the pathogen defence model to be applicable. The same logic must hold for any similar hypotheses that regard heritable personality differences as by-products of other adaptations (**Keller**). We would also like to add that, despite the ingenuity and prominence of the Tooby and Cosmides (1990) article, we are not aware of studies that have directly tested the pathogen defence model. So far, we regard our model as a more plausible alternative.

Environmental challenges for an evolutionary personality psychology

Our model suggests that future phenotypic selection studies should pay special attention to the way that human personality traits interact with specific environments. If spatio-temporal environmental heterogeneity is responsible for maintaining genetic variance in personality traits, then the correlation between a trait and fitness should reverse across some environments. Thus, certain environmental variables should act as statistical moderators of the relationships between personality traits and measures of survival, reproductive success, and/or kin success. A methodological implication is that we need more precise, valid, and evolutionarily informed ways of categorizing and measuring the environmental factors that interact with personality traits to yield adaptive or maladaptive behaviour (**Funder; Matthews; Saad**). Characterizing environmental structure at a useful level of description is a rather old problem that psychologists recognized long ago (see Meehl, 1978), but still struggle to solve (for a notable attempt see Holmes, 2002).

While we cannot offer a panacea, we suggest that an evolutionary framework for personality, richly informed by mid-level adaptationist theories (e.g. concerning kin selection, multi-level selection, reciprocity, sexually antagonistic coevolution, parent-offspring conflict, and life history theory) might help to isolate relevant environmental features. This is because environments can vary in many ways (**Johnson**), but not all of them are equally relevant for understanding the fitness payoffs of particular traits. A useful exploratory heuristic might be to consider “Which variable environmental factors create different adaptive problems that are solved better or worse by individuals with certain personalities?”. For example, big cities with high population densities and anonymous interactions might give Machiavellian cheaters more chances to exploit others than small villages would, in which reputations spread faster through gossip; thus, cities may offer higher fitness payoffs for disagreeable individuals than small villages do. Living in big cities might also imply frequent changes in people’s social networks, which lead to persistent uncertainty about one’s social status and mate value, and

about the pool of available mates, friends, and allies. Neurotic fears of social rejection might be as maladaptive in this context as an indiscriminate tendency to strive for the alpha rank all the time. Harsh and dangerous physical environments likely make social cooperation and mutual support necessary, as do intergroup conflicts over limited resources, so both may favour agreeableness and neuroticism. More generally, the differences in styles of social interaction that are at the core of many personality traits suggest that we should pay special attention to social-environmental factors that may mediate and modulate relationships between personality traits and fitness payoffs. Such a research program is already exemplified by work on sociosexuality as a personality trait with different mating payoffs in different environments (Gangestad & Simpson, 2000).

Saad emphasized the four different roles that environmental factors play in an evolutionary genetic approach to personality. So far, this section only discussed environmental niches, which provide selection pressures. Two of Saad's other environmental roles, the ontogenetic environment of personality development and the current real-time situational context of personality functioning, are combined in our reaction norm model as the "environment" that interacts with the genotype to evoke a behavioural response. These two different functions of the environment as (1) the source of selection pressures and (2) one of the interacting factors in reaction norms (which correspond to the two "Environment" boxes in Figure 3 of the target article) appear to be mixed up in one of **Funder**'s remarks: The ontogenetic and real-time environmental factors that evoke personality differences (an interaction effect) might or might not be the same across different environmental niches that select for or against these differences (a main effect). In future evolutionary genetic studies of personality, it should be helpful to distinguish more carefully between the environmental factors that shape a phenotypic personality trait and the environmental factors that make this trait have certain fitness cost and benefits.

The fourth role of the environment that **Saad** acknowledges is the ancestral environment of evolutionary adaptedness (EEA). Contrary to the commentaries by **Livesley** and **Bates**, the more evolutionarily remote and ancient forms of this environment play a negligible role within an evolutionary genetic perspective on current heritable variation in human personality. Understanding the remote Pleistocene EEA is very useful to explain non-heritable conditional strategies and universal sex differences (**Troisi**, **Saad**), as in mainstream adaptationistic evolutionary psychology. However, genetic variation in contemporary human populations depends on much more recent selection pressures over the last few hundred generations, within the Holocene. Thus, an evolutionary personality psychology may end up paying much more attention to the environment-specific payoffs for personality traits during recent (e.g. Neolithic) prehistory, and even within historically documented civilizations. For example, the divisions of labour and diverse social roles that

emerge within complex hierarchical societies may have permitted a much wider range of personality traits to flourish than would have been possible under small-scale, egalitarian, hunter-gatherer conditions in the Pleistocene.

At which level should we study personality traits from an evolutionary perspective?

We have apparently reached one of those intriguing points in the history of science when there is a mutual recognition between two fields that they have been working on the same problems in slightly different but complementary ways. In this case, the two fields are evolutionary behavioural ecology (the study of variation in animal behaviour) and personality psychology (the study of variation in human behaviour) (**van Oers**). Such times of mutual recognition are always accompanied by initial confusions over terminologies, assumptions, methods, and objectives, before the two fields can take full advantage of each other's insights and findings. Evolutionary ecologists, who usually study animals that cannot report their thoughts or feelings, naturally must focus on observed behaviours, and their correlations, contingencies, and fitness consequences across environments. Since personality psychologists have restricted their studies to a very talkative mammal, they usually prefer to ask their subjects to verbally report their thoughts and feelings, and to look for latent personality constructs that can explain patterns across these self-reports (**Réale**). In terms of the watershed model, evolutionary ecologists usually start their analyses more "downstream" than personality psychologists (**Euler**) — by observing emitted strategic behaviour rather than by recording verbal responses about intended or remembered behaviour.

Evolutionary ecologists usually have a solid training in evolutionary genetics, and they know that selection does not operate on a single trait at a time, but affects all traits that are genetically intercorrelated at once. That is why one objective of animal personality studies is to find behavioural tendencies that are genetically correlated (the "character state perspective", **Dingemanse**; **Sih & Bell**), to understand how patterns of genetic variance and covariance in behavioural propensities fit into the genetic variance-covariance matrix (the "G matrix") that describes all phenotypic traits, whether morphological, physiological, or behavioural. The higher goal is to identify fairly independent dimensions in the G matrix, since these dimensions could also evolve fairly independent of each other. Consequently, these dimensions would constitute the most suitable units of analysis for evolutionary genetic studies (Mezey & Houle, 2003).

Personality psychologists are very familiar with looking for independent dimensions in variance-covariance matrixes, using methods such as factor analysis. However, they started doing so many decades before evolutionary ecologists did, and tended to use phenotypic correlations among cognitive tests, or among self- or peer-ratings on personality-descriptive

adjectives or questionnaire items, rather than among field observations of actual behaviour. This search culminated in the discovery of independent, latent phenotypic dimensions in humans, of which the *g* factor and the Five-Factor Model of Personality (FFM) reached the highest consensus. Most interestingly, these dimensions replicate fairly well on the genetic level (e.g. Yamagata et al., 2006; Plomin & Spinath, 2004), suggesting that research on human personality has already come close to characterizing the genetically correlated dimensions that evolutionary ecologists are still seeking in other species. What is now called the "character state perspective" in evolutionary ecology is so fundamental to personality psychology that we simply took it for granted in our target article. Resolving such terminological and methodological confusions might be the most important first step for interdisciplinary personality research.

When **Livesley** and **McCrae** suggested instead that lower-order, interdependent personality facets may be the best level of analysis for an evolutionary genetics of personality, they may have confused the heritable individual differences relevant to personality research with the species-typical, domain-specific adaptations studied by adaptationistic mainstream evolutionary psychology. A hallmark of adaptations is their complex functional design, which would break down when too much genetic variation is introduced. As a consequence, most heritable individual differences cannot be adaptations (Tooby & Cosmides, 1990), and they cannot be analysed using traditional standards of adaptationism. Rather, they are dimensions of genetic variation that are tolerated within systems of interacting adaptations. For example, humans are likely endowed with adaptations to regulate attachment relationships (**Troisi**), to discover signs of social rejection (Leary & Baumeister, 2000), and to monitor environmental dangers (Nettle, 2006). All these systems are under strong stabilizing selection to function effectively (which maintains their complex adaptive design), but they are still all influenced by individual differences along a heritable dimension called neuroticism. This dimension of personality variation is not at the same level of description as the adaptations themselves, and is maintained by different selective forces – according to our model, by balancing selection given environmental heterogeneity – rather than stabilizing selection for raw functional efficiency.

The lower-level facets of broad personality dimensions show substantial genetic intercorrelations (Yamagata et al., 2006) and will thus show correlated responses to selection. This makes them unlikely to be the most useful units of analysis in studying the evolutionary genetics of personality traits. That being said, we are open to ongoing debate concerning which and how many personality factors best represent independent dimensions of variation in the behavioural aspects of the human G matrix. We concentrated on the dimensions of the FFM, mainly because of their clarity and familiarity, and the rich literature on them. **South and Krueger** as well as **Figueredo & Gladden** suggested that there may be

even higher levels of abstraction than the FFM, as suggested by the evidence of modest phenotypic (Markon, Krueger & Watson, 2005) and genetic intercorrelations between the FFM domains (**Johnson**). One problem with such jumping to a higher level of abstraction is that some genetic correlations may be different from zero at a statistical level of significance, but not at an evolutionary level of significance (cp. **Jang**): these genetic correlations may be caused by environmental factors through gene-environment interactions (GEIs), making them environment- and population-dependent. In the target article, we adopted van Oers et al.'s (2005) argument that genetic correlations due to structural pleiotropy (i.e., shared mechanisms on the endophenotypic level) should not change signs across environments, whereas those due to GEIs should change signs across environments. **Johnson** noted that this criterion might fail to distinguish between types of genetic correlations because people select, create, and evoke their own environments, leading to gene-environment correlations (r_{GE}s). The effects of GEIs and r_{GE}s can easily be confused in empirical results and are difficult to separate (but see Johnson, 2007). **Johnson** argues that r_{GE}s are problematic because they could lead to a homogenization of the populations in certain environments with regard to the traits under study (if its result is that every niche harbours only individuals with exactly those personality trait levels that fit best to the niche's demands). In this case, the genetic correlations could indeed be attenuated by reduced trait variance - possibly down to zero, given perfect r_{GE}s. However, we do not see how the variance reduction within environments that could be caused by r_{GE}s can lead to artificial *sign changes* in genetic correlations across environments. But even if the discriminatory power of the criterion offered by van Oers et al. (2005) is limited in certain cases, we do not follow **Johnson**'s conclusion that this (possible) methodological issue with the detection of structural pleiotropies implies that they are rare in nature.

More critical is **Dingemanse**'s remark that the G matrix is not static and might differ between environments and populations as a result of local selection pressures. Genetic correlations that freely evolve between populations are likely not constrained by structural pleiotropy, but may be the result of selection for limited plasticity. While this does not make them less interesting from an evolutionary genetic perspective, some of our arguments would indeed be invalidated (see **Dingemanse**). We think that the key data to distinguish between structural pleiotropy and selected limits on plasticity would come from cross-cultural studies. If the factorial structure of the behavioural aspects of the G matrix replicate across populations around the world, it is unlikely to reflect recent, local selection pressures. Initial data suggests that the FFM shows good replication of genetic factorial structure across three populations from three continents (Yamagata et al., 2006). This and other studies also suggest that the structure of the behavioural aspects of the G matrix reflects fairly accurately the phenotypic structure of the FFM personality dimensions, which allows us, according to

the protocol suggested by Roff (1997, p. 100), to use phenotypic structures as a surrogate for genotypic structures. Phenotypic data is available for a larger sample of cultures, and again they suggest that the FFM structure replicates rather well across populations (McCrae & Allik, 2002). While more cross-cultural (and within-culture cross-environmental) comparisons of G matrices would be desirable (preferably with designs that are able to differentiate between additive and non-additive genetic variance), these results suggest that the structure of the FFM is caused by structural pleiotropy across behavioural propensities within each of its main dimensions. It remains to be seen, however, if other genetic factor solutions replicate better across cultures, or if the FFM dimensions (and the *g* factor, for which a similar logic holds) already are the best level to study the evolutionary genetics of personality.

Extensions of our evolutionary genetic model of personality

Evolutionary genetics is a rich and complex field, and offers much more to personality psychology than we could cover in our target article. Since evolutionary genetics is novel ground to most personality psychologists, we chose to focus rather simply on the major evolutionary mechanisms that can maintain genetic variation in traits. Also, we tried to rely on theoretical arguments and models that are already well-established and relatively uncontroversial in evolutionary genetics. So, for example, we did not discuss the new but sketchy literature on the maintenance of genetic variance in reaction norms (**Sih & Bell**), where the current conclusions depend on the specific assumptions of complex models and are sometimes contradictory (see de Jong & Gavrilets, 2000, vs. Zhang, 2006). Also, we could only make parenthetical references to some other topics, such as niche picking (a form of active r_{GE}). In the future, our model should be extended by including, among others, a more explicit account of r_{GE}s (**Jang; Johnson; Sih & Bell**), reactive heritability beyond condition-dependency (**Gangestad**), indirect selection in social groups (**Sih & Bell**), and models of genetic variance maintenance in reaction norms (**Sih & Bell**). It should also be contextualized within the broader frameworks of evolutionary game theory (**Sih & Bell**) and life history theory (**Gangestad**). We regard these extensions as generally compatible with our model, but more theoretical and empirical work is needed to see how exactly they would affect our conclusions about the origins and nature of genetic variation in personality. **Dingemanse** reminded us that our model and any future extensions should ideally be tested in formal mathematical models, not just as verbal descriptions. Furthermore, statistical models are needed that allow us to test these relationships against empirical data. First steps in this direction have already been made (**South & Krueger**; **Johnson**; Wolf et al., 1998), but there clearly is plenty of work that still needs to be done.

In itself, an evolutionary genetic model of personality cannot offer a complete theory of personality. It can provide an ultimate perspective on why heritable personality differences exist, how they change over evolutionary time and environments, and which fitness effects they may have. This makes it an important building block of any comprehensive personality theory. In the end, however, any evolutionary genetic model of personality should be complemented by more proximate theories (such as **Matthew**'s) concerning the phenotypic structure, underlying mechanisms, and lifespan development of personality traits. However, as **Funder** correctly noted, our evolutionary genetic model of personality is more compatible with some proximate personality theories than with others, and those theories that contradict it will have to provide alternative accounts for the existence of genetic variance in personality. In the following, we will compare our model to some alternatives suggested in the commentaries.

Alternatives to our evolutionary genetic model of personality

Recent selective sweeps. Mutation-selection balance models assume that within any given population, for any given trait, there is an abstract, idealized, mutation-free genotype that would show optimal adaptation to the population's environmental demands and selection pressures. Applied to the case of human intelligence, mutation-selection balance models suggest that the highest possible *g* level can be attained only when all genes that influence cognitive functioning are free of harmful mutations. **Lee** called this a "Platonic ideal". Both **Bates** and **Lee** pointed to studies suggesting that human general intelligence has been subject to recent selective sweeps and in the midst of a genetic transition (Wang, Kodama, Baldi, & Moyzis, 2006; Evans, Mekel-Bobrov, Vallender, Hudson, & Lahn, 2006; see also Williamson et al., in press). We agree that the hypothetical optimal genotype for optimal intelligence is an oversimplification, and might be better conceptualized as a "moving target". Most mutations in protein-coding and regulatory regions of the genome are harmful, but beneficial mutations are more likely to occur when environments change. Given all the changes that have been occurring in the human ecology during the last 20,000 years, (including larger social groups and mating markets, novel habitats, agriculture, and literacy), it is very likely that some *g*-related mutations have become beneficial and are currently on their way to fixation. These newly-favoured polymorphisms might exist at any current prevalence level, and might have large phenotypic effects, so molecular genetic studies might be better able to identify them.

Beneficial mutations that are on the rise probably contribute to the genetic variance of *g*, but so does a load of many, rare, small-effect harmful mutations. This is not only a widespread empirical conclusion (Plomin et al., 2006), but also a necessary implication if *g* has a large mutational target size. (**Bates** notes that several thousand rare polymorphisms

with strong effects on general intelligence have been identified, but these evolutionary transient, harmful mutations usually cause severe mental retardations, not individual differences in the normal range; see Plomin & Spinath, 2004.) In our view, only a conceptualization of *g* as a downstream trait that represents the functional integrity of large parts of the brain and the genome can explain why there are positive-manifold genetic correlations between different cognitive abilities, why *g* is linked to general phenotypic condition, and why *g* is sexually attractive. It can also explain why trauma often reduces, but never raises, *g* (**Keller**; Keller & Miller, 2006). We do not see how these findings can be reconciled with recent selective sweeps as the only explanation for the heritability of *g*. In an effort to refute our mutation-selection balance account, Bates referred to unpublished evidence of a zero genetic correlation between *g* and fluctuating asymmetry. While we cannot evaluate this study, such a result would challenge only one possible mediator between mutation load and cognitive ability (the construct of "developmental stability"), not the general claim that *g* is under mutation-selection balance. Contrary to **Bates** and **Lee**, we doubt that recent selective sweeps alone can explain most of the genetic variance in *g*, but we believe that such sweeps, in conjunction with mutation-selection balance, may be important, with their relative contributions to be determined by future empirical research.

Cognitive reaction norms. While the *g* factor of intelligence seems to have a direct link to many components of fitness, **Strobel** noted that individual differences in certain lower-order cognitive processes show phenotypic and genetic relations to personality traits – which, in our balancing selection model, should have net fitness neutrality when averaged across all relevant environments. He suggests that such lower-level traits that combine cognitive and personality characteristics may constitute a third category of traits to consider in extending our model. We don't think that such a fundamental modification is necessary. Our two trait categories are basically defined by the selective mechanisms that maintain their genetic variance, not by their apparent psychological nature (i.e., 'cold' and cognitive vs. 'hot' and temperamental). If the lower-order cognitive processes discussed by **Strobel** are indeed under balancing selection and structurally linked to personality traits, they clearly fall in the "reaction norm" category of our model and are likely best conceptualized as facets of certain personality traits. However, since they are usually assessed by cognitive tests that load on the *g*-factor, it might be advisable to control for *g* (which we suggest captures mutation load variance) when their genetic underpinnings and their associations with personality traits are studied.

Gene-environment correlations. It is hardly debatable that humans have been perfecting ways to modify their own environments for thousands of years. Due to technical and cultural innovations, modern humans seldom face unmodified natural ecologies; rather we confront complex built environments and social institutions that have been shaped as our "extended

phenotypes". Consequently, r_{GE}s might be more important for humans than for any other species. **Jang** and **Johnson** argued that modern humans are so adept at creating, selecting, and evoking their own ideal environmental niches that almost no genetic variance in personality is lost to selection now. We agree that modern selection-minimizing environments might be one reason why "maladaptive" genetic variants, like those leading to mental illnesses, are sometimes preserved in the population (**Jang**). However, we doubt that r_{GE}s can fully explain genetic variance in the normal range of personality. The reason is that mere survival is not the only adaptive problem – fitness also depends on success in social competition for resources, status, and mates. In modern societies, few will die because they are ill or incompetent, but many will fail to maximize the quantity and quality of their sexual partners and offspring (e.g. Keller & Miller, 2006). As we argued in our target article, it is likely that personality differences have their strongest effect on fitness in the social domain (see also **Matthews**). As long as diverging interests exist in social groups, no single individual will have full control over his or her social environment (**Sih & Bell**; Penke et al., in press). Some will do better than others, partly due to luck, but primarily due to individual differences in general fitness and variation in the fit between people's personalities and their (socio-)environmental niches. Thus, r_{GE}s may alter or attenuate the selection pressures on personality differences, but they are unlikely to eliminate them. Note also that if r_{GE}s indeed neutralized all selection pressures, personality differences would be under neutral selection, which is, as we argue in our target article and above, inconsistent with empirical evidence. Accordingly, r_{GE}s alone cannot maintain genetic variance.

Antagonistic pleiotropy. **Sih & Bell** remark that antagonistic pleiotropy is still discussed as a viable mechanism for maintaining genetic variance, for example by Roff (2002). While it is true that the final word hasn't been said about this mechanism (especially when trade-offs between more than two traits are involved), even Roff, in a recent review (Roff & Fairbairn, 2007), regards antagonistic pleiotropy alone as very unlikely to explain persistent genetic variance. However, even if some genetic variance in some personality traits is maintained by antagonistic pleiotropy, it would not alter our model dramatically. All it would imply is that environmental heterogeneity is not necessary in these particular cases.

Continua of evolutionary stable strategies. **Keller** lists MacDonald's (1995) hypothesis of weak stabilizing selection on personality traits (which allows for continua of evolutionary stable strategies) as a viable explanation for genetic variation in personality. However, stabilizing selection, even if weak, can only erode, but never maintain, genetic variation (Roff, 2002). The same is true for the related mechanism of correlational selection (**Sih & Bell**; Roff & Fairbairn, 2007). In both cases, either personality traits must be selectively neutral, or the mutational target size of personality traits must be sufficiently large that enough mutational

variance is reintroduced (see **Gangestad**), or some form of balancing selection must occur. This brings us back to the three main mechanisms we discussed.

The K-factor. The r-K continuum describes differences in life-history strategies between species. Each species has evolved a complex functional design that allows for its specific strategy of growth, mating, and parenting. For example, many finely coordinated adaptations in a rat's phenotype interact to let it mature fast, reproduce early and often, develop a small brain, refrain from extensive parental investment, die early, etc., and these systems of adaptations are different from those in an elephant or human. Such an r-K continuum might apply not just to explain between-species differences in life history adaptations, but to explain within-species differences in behavioural strategies and personality differences. **Figueredo & Gladden** suggested that the human G matrix might be characterized by just one principal dimension - the 'K factor' - corresponding to individual differences in life-history strategies and their associated personality traits. Our concerns with this suggestion are mostly theoretical.

We do not see how such an all-encompassing genetic dimension can be maintained by frequency-dependent selection or any other form of balancing selection. Selection cannot change the whole adaptive design of a species back and forth at the level of all genetic loci that influence life history traits, since this would inevitably break up the complex functional coordination of the life history strategy (Tooby & Cosmides, 1990). Instead, balancing selection can only maintain a small set of polymorphisms that act as "switches" between different life-history or behavioural strategies (Kopp & Hermisson, 2006; Turelli & Barton, 2004). These polymorphisms must, through cascading effects in genomic regulatory systems, affect all adaptations involved in the strategy. One – and possibly the only – example for such a potent genetic switch in humans is the SRY gene that guides the sexual differentiation of males and females (Tooby & Cosmides, 1990). In the case of the K-factor, a similar master genomic regulatory switch would have to be identified (and we suspect it already would have been discovered if it existed, given the intensity of gene-hunting for loci with major behavioural effects). Such a master regulatory switch might, for example, affect a range of behavioural traits by regulating testosterone levels and receptor sensitivities during brain development and functioning, since testosterone affects a wide range of sexual, competitive, aggressive, and parental behaviours (Ellison, 2001). However, testosterone-related polymorphisms alone cannot explain all the other traits subsumed in the K-factor, including general intelligence and the dimensions of the FFM. As long as there is no evidence for more potent genetic switches that affect all these traits, we regard K-factor theory as slightly over-ambitious in trying to explain human individual differences. Alternatively, **Gangestad** offers some more detailed considerations on the evolutionary genetics of life-history strategies, including reactive strategy adjustment to one's own

mutation load (i.e., condition-dependency). We encourage future studies to proceed in the directions he suggests.

Conclusion

Our target article introduces a way to study personality from an evolutionary perspective, based on evolutionary genetics. Thereby, it supplements adaptationistic evolutionary psychology with a toolbox for the study of individual differences, and it supplements behaviour genetics and personality psychology with a theoretical framework to understand heritable personality differences. We reviewed three theoretical models for the maintenance of genetic variance in heritable traits, and assessed the available empirical evidence to draw conclusions about the plausibility of each model as it might apply to human personality. While some aspects of the evidence remain weak, the overall pattern of results suggests that balancing selection is more plausible than its alternatives as an explanation for most heritable personality traits, as is mutation-selection balance for general intelligence. It remains to be seen whether our model can integrate future theoretical innovations and empirical findings. We are open to alternatives, extensions, modifications, and most importantly empirical studies with more refined methods that test the predictions of our model.

Clearly, the development of a comprehensive evolutionary personality psychology is a big challenge that is still to be met. Many of the challenges and opportunities in this endeavour lie in its interdisciplinary nature: neither psychologists nor biologists will be able to solve this problem on their own (**van Oers**). The commentaries are encouraging because they suggest that both sides are willing to learn from each other. If basic communicative issues (terminologies etc.) can be resolved, we see many opportunities for fruitful interdisciplinary cooperation, and maybe we can even come a little bit closer to the utopian ideal of consilience (**Euler**).

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Table 1: Mean values for personality variables that show significant differences in parents of twins

	Father's Mean			Mother's Mean		
	Same region *N* = 1433	Different region *N* = 855	Effect size	Same region *N* = 1557	Different region *N* = 950	Effect size
Boredom susceptibility	36.44	37.25**	.113	35.43	35.68	
Experience seeking	31.61	33.76**	.289	29.47	31.62**	.282
Thrill and adventure seeking	28.69	29.50		21.75	22.66**	.118
Test attitude	39.45	38.72*	.086	41.28	40.05**	.143
Somatic anxiety	16.47	16.20		18.16	18.67*	.091

Note. p values next to the means correspondent to the F statistic of the between subjects effects of 'same region'. *p < .05; **p<.01

Table 2: Mean values for personality variables that show significant differences in both twins

	Twin 1 Mean			Twin 2 Mean		
	Same region *N* = 1581	Different region *N* = 955	Effect Size	Same region *N* = 1574	Different region *N* = 954	Effect Size
Boredom susceptibility	38.01	38.56*	.082	37.86	38.77**	.137
Experience seeking	33.95	35.48**	.220	34.12	35.33**	.180
Thrill and adventure seeking	39.09	40.09**	.110	38.83	39.59*	.094
Somatic anxiety	18.66	19.20**	.119	18.66	19.15*	.089

Note. *p* values next to the means correspondent to the *F* statistic of the between subjects effects of 'same region' independent of the effect of sex. $^{*}p < .05$; $^{**}p < .01$

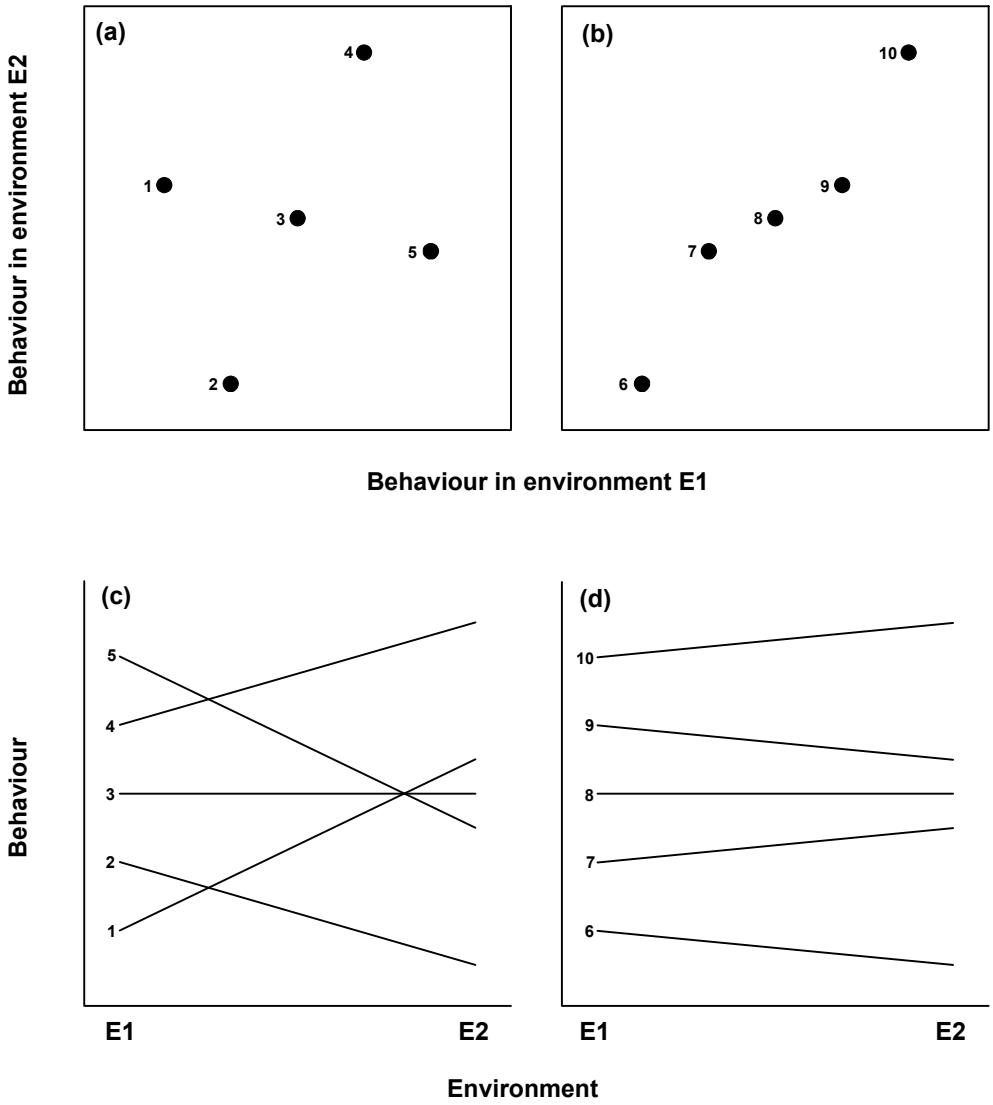

Figure 1: Graphical illustration of genetic variation in personality as viewed from (a-b) a character state approach (both panels plot the breeding values of two behaviours) or (c-d) a reaction norm approach (both panels give breeding values of the same behaviour expressed in two different environments). Note that the two approaches are essentially two sides of the same coin: (a) and (c) depict the same fictional data as do (b) and (d), where each genotype (number) is given either as a dot (a, b) or a line (c, d). Personality does not exist in (a) and (c) but does exist in (b) and (d). Note that the correlation between the breeding values for the behaviours plotted in (a) en (b) represents their additive genetic correlation (Lynch & Walsh 1998).

Part II:

The Life History Approach

Single Attribute Implicit Association Tests (SA-IAT) for the assessment of unipolar constructs: The case of sociosexuality

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Abstract

A major problem with Implicit Association Tests (IATs) is that they require bipolar attributes (e.g., good - bad). Thus, IAT effects for an attribute category can be interpreted only relative to an opposite category. Problems arise if there is no clear opposite category; in this case, a neutral category can be used although it induces systematic error variance and thus reduces validity. The present study suggests that this problem can be solved using Single Attribute IATs (SA-IATs). Sociosexuality (the tendency to engage in uncommitted sex) was expected to be related at the implicit level to stronger stranger - sex associations relative to partner - sex associations. An IAT was constructed that used conversation as a neutral attribute; it showed satisfactory reliability but only low correlations with explicit sociosexuality. An alternative SA-IAT with sex as the only attribute showed a similar reliability but higher correlations with explicit sociosexuality.

Current dual-system models in social cognition research take into account that there are deliberate, reflective as well as spontaneous, impulsive determinants of behavior. Some models such as the one by Strack and Deutsch (2004) assume that information processing giving rise to spontaneous behavior involves implicit mental representations of objects and their attributes in the form of associative networks. The association strength between the mental representations reflects the likelihood that the represented entities co-occur in reality or imagination. Thus, in principle it should be possible to use this information about implicit associations in order to assess individual evaluations and behavioral tendencies, without explicitly asking the respondents to report them.

In recent years, methods such as the Implicit Association Tests (IAT; Greenwald, McGhee, & Schwartz, 1998) have been developed for this purpose. Frequently, these procedures were designed to study implicit attitudes including implicit self-esteem by assessing associations between target objects and attributes along a *good - bad* dimension (see Fazio & Olson, 2003, and Spence, 2005, for reviews). Other studies explored associations between the self as a target concept and behavioral attributes such as *shy - nonshy* or *angry - self-controlled* (e.g., Asendorpf, Banse, & Mücke, 2002; Egloff & Schmukle, 2002; Schnabel, Banse, & Asendorpf, in press). The underlying assumption of these IAT versions is that they predict spontaneous behavior particularly well because they provide direct access to associations between the self and representations of such behaviors.

Evolutionary psychology assumes that many impulsive determinants of human social behavior are based on domain-specific evolved psychological mechanisms that were shaped by selection pressures in our evolutionary past and continue to operate in all humans, or are sex-specific (e.g., Tooby & Cosmides, 1990; Buss, 2003). More recently, attempts have been made by evolutionary psychologists to explain not only sex differences but also systematic interindividual differences within sex by principles of evolution such as frequency-dependent selection, environmentally-contingent strategies, or environment-contingent development (e.g., Buss & Greiling, 1999). The present study combines the social cognition and the evolutionary approaches in an attempt to study impulsive determinants of interindividual differences in sociosexuality.

Sociosexuality

Individuals differ in their tendency to engage in uncommitted sexual activity, a disposition Kinsey (Kinsey, Pomeroy, & Martin, 1948; Kinsey, Pomeroy, Martin, & Gebhard, 1953) termed sociosexual orientation or *sociosexuality*. Sociosexuality is conceptualised as a personality dimension, with the poles labeled “restricted” (monogamous) vs. “unrestricted” (promiscuous) sociosexuality. Based on the observation that sociosexual behaviors, attitudes

and fantasies tend to correlate, Simpson and Gangestad (1991) developed the Sociosexual Orientation Inventory (SOI), a 7-item self-report questionnaire that combines measures of sociosexual attitudes, behaviors and fantasies to an overall score. The SOI has been applied in over 40 published studies (reviewed in Simpson, Wilson, & Winterheld, 2004), including a large-scale intercultural study that confirmed its reliability and validity across 48 nations (Schmitt, 2005). The latter study also showed that men universally have a more unrestricted sociosexual orientation than women (an overall effect size of d=0.74), a sex difference that is expected from evolutionary theorizing (Trivers, 1972; Buss & Schmitt, 1993).

The heterogeneity of the SOI due to the inclusion of both sociosexual attitudes and behaviors has sometimes been criticized (e.g., Townsend, Kline & Wasserman, 1995). We therefore first examined the factorial structure of sociosexuality in an extended version of the SOI, the Sociosexuality Scale (SS) by Bailey, Kirk, Zhu, Dunne, and Martin (2000).

Sociosexuality is distinct from general sex drive or libido (Ostovich & Sabini, 2004), and unrelated to the interest to engage in sexual activity with a committed relationship partner (Simpson & Gangestad, 1991). Indeed, sexual motivation towards strangers appears to serve completely different functions than sexual motivation in committed relationships (Buss & Schmitt, 1993; Klusmann, 2002).

Assessment of Implicit Sociosexuality

If interindividual differences in sociosexuality are primarily based on evolved mechanisms at the level of impulsive information processing, they are a prime candidate for the application of social cognition methods such as Implicit Association Tests. However, we are not aware of any such study in the literature. Our attempt to study implicit sociosexuality was guided by four assumptions. First, the evolved mechanism underlying sociosexuality is the desire for sexual variety, a motive to quickly engage in sexual activity with members of the preferred sex, even if they are totally unacquainted (Buss & Schmitt, 1993; Schmitt, Shackelford, Duntley, Tooke, & Buss, 2001; Schmitt et al., 2003). Second, therefore, sociosexuality is characterized at the level of impulsive information processing (Strack & Deutsch, 2004) by the strength of the association between *stranger* and *sex*. That is, when unrestricted males and females meet strangers, they associate sexual thoughts and feelings with them more easily than restricted males and females.

Third, because of the theoretically expected higher sociosexuality of males that has been strongly confirmed at the explicit level (Schmitt, 2005; Schmitt et al., 2003), males should show, on average, stronger *stranger* - *sex* associations than females. And fourth, the correlation between measured explicit sociosexuality and the measured association strength between *stranger* and *sex* should be moderately positive because both measures relate to

the same construct but show method-specific variance in the explicit measures (e.g., tendencies to admit or to exaggerate sexual motives) and in the implicit measures.

Thus, the key task was to construct a test that assesses the individual strength of the association between *stranger* and *sex*. Because of the notoriously low reliability of affective or semantic priming as a method for the assessment of interindividual differences (see, e.g., Spence, 2005), we initially attempted to construct an Implicit Association Test (IAT; Greenwald et al., 1998) that contrasts the association strength between *stranger* and *sex* with the association strength between *sex* and a control category that was generally linked with *sex* but not specifically linked with *sex* in unrestricted individuals. We chose *partner* as such a control target category because *partner - sex* is an ubiquitous association and because we did not expect a stronger *partner - sex* association for unrestricted individuals because explicit sociosexuality is unrelated to sexual interest in committed relationships (Simpson & Gangestad, 1991).

Another requirement for IATs is an opposite or at least neutral attribute category (in the present case: for *sex).* We used *conversation* as such an attribute because it can be easily associated with both strangers and partners and because we asssumed that *conversation* is sexually neutral and therefore unrelated to sociosexuality. Thus, our sociosexuality IAT used categories that referred to social interaction: the bipolar target categories *stranger - partner* that primarily differ with regard to the unfamiliarity of the social interaction partner, and the attribute categories *sex - conversation* that primarily differ with regard to the sexual nature of the social interaction.

Study 1: IAT

A sociosexuality IAT aiming at assessing the association strength between *stranger* and *sex* relative to the association strength between *partner* and *sex* was developed in a laboratory experiment, and subsequently tested on the internet. *Conversation* was chosen as a sexually neutral control category. Explicit ratings of the association of *sex* and *conversation* with an opposite-sex stranger in a hypothetical situation and the Sociosexuality Scale by Bailey et al. (2000) that includes the Sociosexual Orientation Inventory by Simpson and Gangestad (1991) served as validation criteria.

Method: Laboratory IAT Study

Adult males and females were invited to participate in a laboratory study on sexuality through advertisements in local magazines or personal contacts. Most participants were students (less than 10% psychology students). Participants either received course credits, coupons for a local movie theater, or participated in a lottery with attractive prizes. The present study refers only to those participants that (a) aged 18 - 39 years, (b) were

heterosexual and sexually experienced according to self-report, and (c) had an overall error rate not above 15% in the sociosexuality IAT (see below). These criteria were met by 50 males and 44 females; mean age was 24.0 years (*SD* = 4.3).

Participants answered a few questions concerning personal information such as age, sex, sexual orientation, and relationship status, completed the *sociosexuality IAT*, and subsequently answered various questionnaires including a *sociosexuality situation rating* and the *Sociosexuality Scale*, in this sequence. Thus, the implicit sociosexuality measure was assessed before the two explicit sociosexuality measures. All items were answered on a computer.

Sociosexuality IAT. This IAT was constructed closely following the procedure outlined by Greenwald et al. (1998). The target-concept discrimination was *partner - stranger*, and attributes were *sex - conversation*. In a first step, participants discriminated *partner - stranger*, then *sex - conversation*. In the initial combined task, they discriminated *partner - sex* from *stranger - conversation*. Subsequently, they discriminated *partner - stranger* in reversed order, and finally *stranger - sex* from *partner - conversation* (reversed combined task; see Table 1). The 80 test trials in each combined condition were preceded by 40 training trials. The IAT effect was computed by subtracting the mean reaction time in the test trials of the reversed combined task from the mean reaction time in the test trials of the combined task; thus, positive IAT effects indicate faster associations between *stranger* and *sex* than between *partner* and *sex*, assuming that *conversation* is equally associated with strangers and partners.

Participants used the letter *A* on the left side of the keyboard and the number *5* on the right-side numeric keypad for discrimination. The target and/or attribute category names were presented in the left and right upper corners of the computer screen throughout each task. The stimuli (category exemplars; see Table 2) were presented in the center of the screen until the participant responded. In the two combined tasks, the stimuli alternated between target and attribute. Target and attribute categories were randomized in order within six blocks of 20 trials. Interstimulus interval was 250 ms; after an incorrect response, the word *FEHLER* (German for *error*) immediately replaced the stimulus for 300 ms. Because this study focuses on interindividual differences, all participants received the blocks and the stimuli in the same order to minimize interindividual variance due to order effects. Thus, the IAT means are confounded with block order and can be interpreted only with regard to interindividual and group differences, not absolutely.

Participants were instructed to respond as quickly and accurately as possible. Their responses were recorded using Experimental Run Time System Software (Beringer, 1994). In keeping with Greenwald et al. (1998), the first two responses in the combined tasks were not analyzed, response latencies below 300 ms were recoded as 300 ms, and latencies

above 3,000 ms were recoded as 3,000 ms; incorrect responses were treated as missing values. The raw latencies were used only for descriptive purposes. All other statistical analyses were based on log-transformed latencies to correct for the skewed latency distribution.

Sociosexuality Situation Rating. Participants were asked to imagine a situation where they are alone in a train compartment with an attractive stranger of the opposite sex, and to rate the extent to which they would associate this situation with 20 items on a 5-point scale (*not at all - very much*). Of the 20 items, 10 were the attribute stimuli for *conversation* and *sex* in the sociosexuality IAT (see Table 2) which were randomly mixed with 10 distractor items (e.g., window, smoking). The 5 *conversation* ratings (α=.94) and the 5 *sex* ratings (α=.94) were aggregated, serving as explicit measures of the tendency to associate *conversation*, or *sex*, with the stranger situation.

Sociosexuality Scale. The 20-item Sociosexuality Scale (SS) by Bailey et al. (2000) was translated into German. It consists of the items of the Sociosexual Orientation Inventory (SOI; Simpson & Gangestad, 1991), 12 items in a yes/no format from Eysenck (1976) that assess sociosexual attitudes and a further open question about the lifetime number of sexual partners. A factor analysis with varimax rotation identified, according to the scree plot, two orthogonal factors which could be clearly interpreted as sociosexuality attitude (highest loading item *Sex without love is ok*, explained variance 18.9%) and sociosexual behavior (highest-loading item *During your entire life, how many partners of the opposite sex have you had sexual contact with?*, explained variance 14.6%).

Therefore we constructed from the *z*-standardized items that loaded above .50 on one factor and below .30 on the other factor two short subscales of the SS, the *sociosexual attitude scale* (items no. 3, 9-12, 14 of the original SS) and the *sociosexual behavior scale* (items no. 16-19 of the original SS). Because the items of the sociosexual behavior scale were strongly skewed and included zero responses, they were submitted to a log+1 - transformation. The resulting scales showed sufficient reliability despite their shortness, α=.79 for attitude, α=.72 for behavior. The two subscales correlated significantly but not highly, r=.34, p<.001. To compare our findings with other studies, we also report results for the SOI score (α=.69).

Method: Internet IAT Study

A similar study was conducted online on www.psytests.de, the online portal for internet studies of the Institute of Psychology, Humboldt University. The website was also linked with multiple German websites specializing in psychological experiments and tests. Despite former preconceptions, evidence is accumulating that online studies can provide valid data for research on implicit associations (Nosek, Banaji, & Greenwald, 2002), personality

(Gosling, Vazire, Srivastava, & John, 2004), and sexuality (Mustanski, 2001). The study was implemented in line with the guidelines on internet research proposed by Michalak and Szabo (1998) and the recommendations given by Kraut, Olson, Banaji, Bruckman, Cohen, and Couper (2004).

After basic demographic questions, the sociosexuality IAT was given, followed by, among other measures, the Sociosexuality Scale. Both the implicit and explicit measures were analyzed exactly as in the laboratory study. The explicit ratings were programmed in HTML and php. The IAT was programmed as a JAVA applet, which was embedded in the web page that the participants loaded into their browsers. When the IAT was successfully finished, the results were uploaded to the website. The JAVA applet used an inaccurate-timing filter (Eichstaedt, 2001) such that response time biases due to, e.g., the parallel execution of other programs were minimal. Participants were prompted to reduce any sources of environmental disturbances during the study and asked to participate only if they had enough time and privacy.

During 17 days, 187 website visitors completed all parts of the study. Selected for the final sample were all sexually experienced heterosexuals aged 18 - 39 years (47 males, 89 females); mean age was 23.7 years (*SD*=5.2). The sample did not differ significantly from the laboratory sample with regard to age and the number of lifetime sexual partners (all $p>.10$).

Results

In the laboratory IAT, 4 participants (4.3%), and in the internet IAT, 3 participants (2.2%) showed more than 15% incorrect responses during the combined blocks; they were excluded from further analysis. As Table 3 indicates, the laboratory and the internet IAT showed similar means, *SD*s, error rates, and internal consistencies α; *t* tests confirmed this for the mean IAT effect and the error rate, $t<1$ in both cases. Also, the correlations with the explicit sociosexuality scales were not significantly different as confirmed by *z* tests for differences between correlations. Thus, the internet method yielded virtually identical results as the laboratory method.

Concerning the validity of the IAT, the results were disappointing because the correlations with the explicit sociosexuality scales (SOI and the behavioral and attitudinal subscales of the SS) were not significant in all 6 cases (the mean correlation was .04). Also, the sex difference was not even marginally significant for both the laboratory IAT and the internet IAT, $p>.10$ in both cases. This result suggested that there was perhaps a problem with the *conversation* category. If *conversation* is positively related to implicit sociosexuality, this would at least partly explain the low correlation between the IAT and the sociosexuality scales.

In order to test this *a posteriori* hypothesis, the stranger situation ratings in the laboratory study were analyzed (situation ratings were not assessed in the internet study). The *conversation* ratings correlated clearly positively with the *sex* ratings, r=.41, p<.001. Thus, participants who more strongly associated *sex* with the stranger situation also tended to more strongly associate *conversation* with it, and vice versa. However, the SOI scores were only associated with the *sex* ratings. They correlated significantly, r=.26, p<.05, with the *sex* ratings, not at all with the *conversation* ratings, r=.00, and significantly with the difference score *sex - conversation*, r=.26, p<.05. Thus, as expected, explicit sociosexuality was related to the explicit tendency to associate sex with this situation, but not conversation. In other words, *conversation* was a neutral category, not an opposite category, with regard to explicit sociosexuality. As Table 3 indicates, the sociosexuality IAT replicated this pattern. It correlated r=.19, p=.07, with the *sex* rating, and r = -.03, *ns*, with the *conversation* rating; the correlation with the difference score *sex - conversation* was r=.21, p<.05.

Together, these results for the stranger situation ratings suggest that *conversation* is a neutral category with regard to sociosexuality at both the explicit and the implicit level. The rather high correlation of .41 between the ratings of *conversation* and *sex* seems to be due to shared method variance that is independent of sociosexuality, particularly situation-specific tendencies to engage in any activity with strangers.

Discussion

This study has replicated for a laboratory version and an internet version descriptive indices of an sociosexuality IAT that aims at assessing the association between *stranger - sex* relative to *partner - sex*, with *conversation* serving as a neutral category. For young adult samples, the mean, the standard deviation, and a satisfactory error rate and reliability were replicated. However, at the same time this study also replicated that this IAT failed to show any significant correlations with three explicit sociosexuality scales. Weak evidence for the IAT's validity was only found for the ratings of a potential interaction with an opposite-sex stranger; the IAT was significantly related to *sex* minus *conversation* ratings that used the IAT stimuli for these categories as items. Together, these results point to a weak validity of the IAT that was only revealed for an explicit measure that was more closely matched to the IAT procedure than the traditional sociosexuality scales. These situation ratings also confirmed that *conversation* is a neutral category with regard to both implicit and explicit sociosexuality because both explicit sociosexuality and the IAT correlated virtually zero with the *conversation* ratings while showing at least marginally positive correlations with the *sex* ratings.

These results suggested to us that the validity of the sociosexuality IAT was suppressed by individual differences in the tendency to associate *conversation* more with *strangers* than

with *partner*, individual differences that were irrelevant for sociosexuality but confounded with the IAT scores. Therefore we constructed a sociosexuality Single Attribute IAT (SA-IAT) that relied solely on the attribute category *sex* but was otherwise as much comparable with the sociosexuality IAT as possible.

Study 2: SA-IAT

Method

For this study, the sociosexuality IAT was modified to a single attribute IAT. Target concepts were again *partner* and *stranger*, but only *sex* served as the (unipolar) attribute; for these 3 categories, the same stimuli were used as in the sociosexuality IAT. The testing and analysis procedures were the same as for the sociosexuality IAT except that (a) the attribute discrimination and the reverse attribute discrimination were dropped, and (b) only *sex*-related stimuli were presented in the attribute conditions (thus, each of the 5 *sex* stimuli occurred twice as often as in the sociosexuality IAT). Table 4 presents the SA-IAT task; it is structurally highly similar to the Single Target IAT (ST-IAT) by Wigboldus, Holland, and van Knippenberg (2005) except that the asymmetry in this variant of the IAT refers to attributes rather than targets.

Because we were initially concerned that participants would become bored during the many trials of this simplified procedure, and because Wigboldus et al. (2005) used only 40 trials in the combined blocks of their ST-IAT, we first implemented a short version of the SA-IAT with only 20 trials in the target discrimination task and only 60 trials in the combined tasks. Because of reliability problems we subsequently used the full procedure. Below we refer to these two versions as the *short version* and the *full version*.

The short version was tested on 17 days immediately preceding the internet IAT study, thus, on as many days as the internet IAT, resulting in 236 completed tests. The full version was tested during a whole year, starting after the IAT testing, because it was found to be advantageous to the short version as shown in the result section. To provide a fair comparison between short and full version, only the tests of the full version completed on the first 17 days of testing are considered here (171 tests). The final sample consisted of 315 sexually experienced heterosexuals aged 18 - 39 years (56 males and 117 females, mean age 23.9 years, *SD*=5.4, short version; 54 males and 89 females, mean age 24.3 years, *SD*=5.9, full version). The internet samples in Studies 1 and 2 (IAT, short SA-IAT, full SA-IAT) did not differ significantly with regard to sex composition, age, highest achieved educational level, and number of lifetime sexual partners.

Results

Because of error rates above 15% in the SA-IAT, 9 participants (5.2%) were excluded for the short SA-IAT, and 4 participants (2.9%) for the full SA-IAT. Table 5 presents the results for these two SA-IAT versions that can also be directly compared with the results for the two IAT versions in Table 3. Table 5 indicates that the short and the long versions had a mean close to zero and similar standard deviations and error rates. However, the long version was more reliable, which can be attributed to the double number of trials in each combined task. Indeed, the Spearman-Brown formula predicts a reliability of .81 for the full version on the basis of the .68 reliability for the short version. An inspection of the corrected block - total correlations for the 6 20-trial blocks to which the reliability of the full version refers indicated that these correlations were similarly high; in particular, they did not decrease toward the end of the test trials. Because of the higher reliability of the full version, it is not surprising that the correlations with the sociosexuality scales were somewhat higher for the full version.

When the SA-IAT findings for the full version are compared with the internet IAT results (to avoid methodological differences with the laboratory IAT), the SA-IAT showed a similar error rate and reliability, significantly higher correlations with the SOI scale, z=2.48, p<.05, the behavioral SS subscale, z=2.46, p<.05, but not the attitudinal SS subscale, z=1.57, *ns*. The SA-IAT also showed a significantly more positive mean, t(270)=9.09, p<.001, and a smaller standard deviation, F(1,270)=10.93, p<.001; the interindividual variance was reduced to 60% of the IAT variance. Finally, a comparison of the mean reaction times for the 80 test trials between the internet IAT and the full SA-IAT revealed significantly faster reactions in the SA-IAT (for the first combined block: IAT, M=795.2 ms, SD=165.7, SA-IAT, M=750.4 ms, SD=240.3, t(270)=2.90, p<.005, d=0.35; for the reversed combined block: IAT, M=921.8 ms, SD=197.6, SA-IAT, M=741.2 ms, SD=228.8, t(270)=8.87, p<.001, d=1.08). The faster responses particularly for the reversed combined block can be attributed to the easier SA-IAT task, particularly regarding the reversal of a single attribute in the SA-IAT versus two targets in the IAT (see Tables 1 and 4).

An analysis of the sex differences in the two SA-IAT versions was consistent with the hypothesis that the full version showed a higher validity than the short version. Whereas the sex difference for the short version was not significant, p>.10, which was consistent with the IAT, the full SA-IAT showed the expected sex difference. Males had significantly higher implicit sociosexuality scores than females (for males, M=21.4 ms, SD=128.0; for females, M=-13.0 ms, SD=97.6; t(137)=2.01, p<.05, d=0.34) which was slightly smaller than the effect at the explicit level for Germany of d=0.48 (Schmitt, 2005). Thus, only the full SA-IAT version showed a significant, moderate sex difference.

In order to test whether this sex difference was only due to the correlation of the SA-IAT with explicit sociosexuality, an analysis of covariance was conducted, with sex as the

independent factor and the SOI score as the covariate. The sex effect for the SA-IAT remained nearly unchanged, $F(1,136)=3.46$, $p=.06$, $d=0.32$. Thus, it cannot be attributed to a mediation through explicit sociosexuality.[1]

Discussion

The findings for the two SA-IAT versions suggest that (a) the full version should be preferred to the short version because of the higher reliability of the full version, and (b) the SA-IAT is a more valid measure of implicit sociosexuality than the IAT.[2]

The much larger interindividual variance of the internet IAT, as compared to the full SA-IAT, suggest that the IAT effects were confounded with interindividual differences to associate *conversation* more with a stranger versus a partner. As the stranger situation ratings in the laboratory study suggested, these additional interindividual differences were largely independent of the target interindividual differences, namely to associate *sex* more with a stranger than with a partner. Due to this additional variance component, the variance was higher in the IAT than in the SA-IAT. The more negative mean in the IAT as compared to the SA-IAT suggests that the confounding component in the IAT had a negative mean, that is, participants overall associated *conversation* less strongly with a partner than with a stranger, slowing down the reversed combined task which is interpreted in terms of implicit sociosexuality as low implicit sociosexuality.

It should be noted that this is by no means the only possible interpretation. Alternatively or additionally, a comparison of the reaction times between the IAT and the SA-IAT suggests that the participants in the SA-IAT profited more from the simpler task reversal, speeding up their responses in the reversed combined block, which is interpreted as higher implicit sociosexuality. Also, the higher variance of the IAT as compared to the SA-IAT may be partly due to higher task shift costs in the IAT, a cognitive variable that has been shown by Mierke and Klauer (2003) to confound IAT responses and to increase their variance. These task shift costs refer to the alternating between target and attribute stimuli in the combined tasks.

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[1] The effect sizes remained highly similar with regard to reliability, correlation with explicit sociosexuality, and sex differences when the full SA-IAT data obtained during a whole year were analyzed, and these effects were all confirmed at the $p < .001$ level due to the much larger sample (N=1611).

[2] The IATs and SA-IATs were also analyzed using the *D*-measure proposed by Greenwald, Nosek and Banaji (2003) where the difference between the mean log-transformed latencies in the combined tasks is divided by the intraindividual standard deviation of these latencies. The *D* measure correlated above .95 with the traditional difference measure in all four studies, and yielded results that were highly similar to those obtained by the traditional unstandardized difference measure. Therefore, we report here only the results for the traditional measure.

Although both the IAT and the SA-IAT were designed such that targets and stimuli alternated constantly from trial to trial, the associated task shift costs may have been lower for the SA-IAT because the task was simpler.

In any case, an additional irrelevant variance component in the IAT might have suppressed its validity. Psychometric considerations support this view. If a variable X with variance s^2 correlates *r* with a criterion Z, the sum of X and a variable Y with the same variance s^2 correlates $r\sqrt{1/2}$ with Z *if* Y is uncorrelated with both X and Z (a mathematical truth that can be proved algebraically). For example, applying this formula to the SA-IAT correlation of .20 with the SOI yields an expected IAT - SOI correlation of .14 if the IAT effect can be represented as the sum of the SA-IAT effect plus the effect of an uncorrelated variable with the same variance as the SA-IAT.

It is important to note that a higher validity of the SA-IAT cannot be claimed only on the basis of the implicit - explicit correlations because the true correlation between implicit and explicit sociosexuality is unknown. If this correlation would be zero, the correlational results would suggest that the SA-IAT is more strongly related to explicit sociosexuality because the procedure might be more transparent to many participants. However, the sex difference in the full SA-IAT supports the view that the SA-IAT was in fact more valid than the IAT. As expected, males showed a larger SA-IAT effect than females, and when explicit sociosexuality was controlled in an analysis of covariance, the sex difference for the SA-IAT remained nearly unchanged. Thus, the sex effect for the full SA-IAT was not mediated by explicit sociosexuality. In contrast, the sociosexuality IAT did not show this expected sex difference.

General Discussion

Problems can arise for Implicit Association Tests if there is no clear opposite category. In this case, a neutral category can be used although it induces systematic error variance and thus reduces validity. The present study suggests that this problem can be solved using Single Attribute IATs (SA-IATs). Sociosexuality was expected to be related at the implicit level to stronger *stranger - sex* associations relative to *partner - sex* associations. An IAT was constructed that used *conversation* as a neutral attribute; it showed satisfactory reliability but only low correlations with explicit sociosexuality, and failed to show a theoretically expected sex difference. An alternative SA-IAT with *sex* as the only attribute showed a similar reliability but higher correlations with explicit sociosexuality, and confirmed the expected sex difference even when explicit sociosexuality was controlled.

Whereas a Single Attribute IAT was superior to a traditional bipolar attribute IAT in the present study, we cannot exclude the possibility that another sociosexuality IAT with an opposite attribute to *sex* that is more strongly associated with *stranger* by those low in

sociosexuality than by those high in sociosexuality, is more valid than the present sociosexuality IAT. In such a case, the construct of sociosexuality would be better compatible with the bipolar attribute assumption underlying IATs. However, it is hard to imagine that such a "naturally opposite" attribute to *sex* exists for sociosexuality.

Apart from this construct-specific problem, we do not claim that Single Attribute IATs are always a good solution for the assessment of implicit associations involving unipolar attributes. Instead, we consider the Single Attribute IAT option as an interesting hypothesis that should be tested for a wide variety of constructs. Such studies could also study correlations between an IAT and a SA-IAT for the same construct by assessing both in counterbalanced order within sex.

Last but not least, we would like to point out a problem that even Single Attribute IATs cannot solve: the problem of unipolar targets. Our SA-IAT was designed to assess the relative association strength of *sex - stranger* as compared to *sex - partner*, assuming that the *sex - partner* association is not positively related to sociosexuality because explicit sociosexuality has been shown to be largely independent of explicit reports of sexual interest in committed relationships. This assumption could be empirically tested at the explicit level similarly to our test of the association between sociosexuality and *conversation*.

Ultimately, however, it would be necessary to assess the *sex - stranger* association independently from the *sex - partner* association at the implicit level. This would require reliable and valid "Single Attribute Single Target Association Tests", i.e. procedures that purely asses associations between two concepts. At a first glance, priming seems to be a candidate method, but the reported reliabilities for interindividual differences assessed with priming are discouraging (Spence, 2005). We consider the development of new instruments for the reliable assessment of interindividual differences in the strength of simple associations between one target concept and one attribute concept as an important task for the years to come.

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Table 1: Implicit Association Test for Sociosexuality: Task Sequence

Block	No. of trials	Task	Response key assignment	
			Left key	Right key
1	40	Target discrimination	Stranger	Partner
2	40	Attribute discrimination	Conversation	Sex
3	40+80	Initial combined task	Stranger, conversation	Partner, sex
4	40	Reversed target discrimination	Partner	Stranger
5	40+80	Reversed combined task	Partner, conversation	Stranger, sex

Table 2: *Implicit Association Test for Sociosexuality: Stimuli (original German stimuli in parentheses)*

Partner	Stranger	Sex	Conversation
Partner (Partner/in)	Stranger (Fremde/r)	Sex (Sex)	Talk (Gespräch)
Steady partner (Feste/r Partner/in)	Unknown person (Unbekannte/r)	Seduce (Verführen)	Conversation (Unterhaltung)
Lifetime companion (Lebenspartner/in)	Unfamiliar person (Unvertraute/r)	Lust (Lust)	Chat (Geplauder)
Steady relationship (Feste Beziehung)	New acquaintance (Neue/r Bekannte/r)	Erotic (Erotik)	Talking (Reden)
Lifemate (Lebensgefährte/in)	New man/woman (Neue/r Mann/Frau)	Arousal (Erregung)	Speaking (Sprechen)

Table 3: *Results for the Sociosexuality IAT: Effect, error rate, reliability, and external correlates*

		Effect (ms)		Error rate[a]		Reliability	Correlation *r* with				
IAT	*N*	*M*	*SD*	*M*	SD	α[b]	SOI	SS_{att}	SS_{beh}	Conv	Sex
Laboratory	94	-156.2	148.3	5.3%	3.3%	.81	.13	.20#	.07	-.03	.19#
Internet	133	-126.6	141.8	5.4%	3.6%	.75	-.06	.02	-.13	-	-

Note. SOI = Sociosexual Orientation Inventory sum score, based on the *z*-transformed items of the SOI

SS_{att} = sociosexual attitude subscale of the SS; SS_{beh} = sociosexual behavior subscale of the SS;

Conv = situation rating conversation; Sex = situation rating sex

[a] Percentage of incorrect responses in the combined tasks.

[b] Reliability was evaluated with regard to the four 20-trial blocks in the test trials of the combined tasks.

# $p < .10$.

Table 4: *Single Attribute IAT for Sociosexuality: Task Sequence*

Block	No. of trials[a]	Task	Response key assignment	
			Left key	Right key
1	40	Target discrimination	Stranger	Partner
2	40+80	Initial combined task	Stranger	Partner, sex
3	40+80	Reversed combined task	Stranger, sex	Partner

[a] Half as many trials in each condition for the short version.

Table 5: *Results for the Sociosexuality SA-IAT: Effect, error rate, reliability, and external correlates*

		Effect (ms)		Error rate[a]		Reliability	Correlation *r* with		
SA-IAT	*N*	*M*	*SD*	*M*	SD	α	SOI	SS_{att}	SS_{beh}
Short	163	-1.95	101.1	5.7%	3.8%	.68[b]	.20*	.14	.14
Full	139	-0.64	110.3	4.5%	2.6%	.82[c]	.21*	.19*	.14

Note. SOI = Sociosexual Orientation index, based on the *z*-transformed items of the SOI; SS_{att} = sociosexual attitude subscale of the SS; SS_{beh} = sociosexual behavior subscale of the SS.

[a] Percentage of incorrect responses in the combined tasks.

[b] Reliability was evaluated with regard to the 3 20-trial blocks in the combined task.

[c] Reliability was evaluated with regard to the 6 20-trial blocks in the combined task.

* $p < .05$. ** $p < .01$

Beyond global sociosexual orientations: A more differentiated look at sociosexuality and its effects on courtship and romantic relationships

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Key words: Sociosexuality; Sociosexual Orientation Inventory (SOI); mating tactics; flirting; romantic relationships; personality development; evolutionary psychology

Abstract

Sociosexuality is usually assessed as the overall orientation towards uncommitted sex. While often useful, this global approach masks the theoretically meaningful, unique contributions of its components. In a large online study (N = 2,708) and a detailed behavioral assessment of 283 young adults (both singles and couples) with a 1-year follow-up, we showed discriminant validity for behavioral experiences, attitudes towards uncommitted sex, and sociosexual desire (all measured by a revised version of the Sociosexual Orientation Inventory, the SOI-R) regarding both sex differences and many established correlates of sociosexuality. Furthermore, these three facets played unique roles in the predictions of observed flirting behavior when meeting an attractive opposite-sex stranger, even down to the level of objectively coded behaviors, and in the prediction of the self-reported number of sexual partners and changes in romantic relationship status over the following year. They also showed distinct developmental patterns, degrees of assortative mating, and effects on a romantic partner. Implications for the evolutionary psychology of mating tactics are discussed.

Kinsey's studies on normative sexuality (Kinsey, Pomeroy & Martin, 1948; Kinsey, Pomeroy, Martin & Gebhard, 1953) were the first to provide scientific evidence that promiscuity is a fairly frequent phenomenon (a finding later confirmed, for example, by Laumann, Gagnon, Michael & Michaels, 1994, and Schmitt, 2005a). Kinsey introduced the term "sociosexuality" to describe individual differences in people's willingness to engage in uncommitted sexual relationships. The construct of sociosexuality received much interest in various branches of psychology when Simpson and Gangestad (1991) provided a short self-report measure of global sociosexual orientations, the *Sociosexual Orientation Inventory* (*SOI*). It assesses sociosexuality along a single broad dimension, with high scores indicating an *unrestricted* sociosexual orientation (i.e., an overall more promiscuous behavioral tendency) and low scores indicating a *restricted* sociosexual orientation. The SOI proved to be a valuable instrument in more than forty published studies (reviewed in Simpson, Wilson & Winterheld, 2004), where it showed relations to, for example, mate choice preferences (Simpson & Gangestad, 1992; Fletcher, Simpson, Thomas & Giles, 1999), courtship behaviors (Simpson et al., 1993, 1996, 1999), romantic relationship stability (Simpson, 1987) and quality (Simpson & Gangestad, 1991; Ellis, 1998; Jones, 1998), and high-risk sexual behavior (Seal & Agostinelli, 1994). Another important reason for the success of the SOI was that it became the standard operationalization of individual differences in the study of long-term versus short-term mating tactics in evolutionary psychology (e.g. Schmitt, 2005a). This allowed sociosexuality research to take place within an elaborated theoretical framework (Trivers, 1972; Buss & Schmitt, 1993; Gangestad & Simpson, 2000). However, despite its undeniable success, a limitation that runs through the history of sociosexuality research like a central thread is the almost exclusive focus on sociosexual orientations as a unitary behavioral tendency (Asendorpf & Penke, 2005; Webster & Bryan, in press; Townsend, Kline & Wasserman, 1995). In the current article, we argue for a more differentiated perspective.

Global Sociosexual Orientations

When biologist Alfred Kinsey (Kinsey et al., 1948, 1953) first wrote about sociosexuality, his approach to human sexuality was the standard biological approach to an unknown territory (which human sexuality was at that time): as descriptive and objective as possible. Consequently, he introduced sociosexuality as a global behavioral tendency; his interests in underlying causes and mechanisms were fairly limited. Simpson and Gangestad (1991) appeared to share this global perspective when they developed the SOI. Even though they acknowledged different aspects of sociosexuality ("overt" and "covert" behaviors, attitudes), their endeavors were guided by the explicit aim of developing a broad measure of global sociosexuality (p. 883). As a result, the SOI total score became an amalgam of (1) past sociosexual behaviors (items 1 and 3), (2) future behavioral expectancy (item 2), (3) the

frequency of unrestricted fantasies (item 4), and (4) attitudes towards sociosexuality (items 5, 6, and 7) (Table 1).

Despite the obvious psychological heterogeneity of these items, the fact that the SOI remained the sole operationalization of sociosexuality corroborated the implicit equation in the literature of sociosexuality with the SOI total score. In addition, the global conceptualization of sociosexuality happened to fit quite smoothly with the evolutionary psychology of human mating that developed around it in the following years, which tended to focus more on the environmental and personal factors that determine global sociosexual orientations (Gangestad & Simpson, 2000; Schmitt, 2005a) than on the evolved psychological mechanisms that allow individuals to choose their mating tactics adaptively (Miller, 1997; Mata, Wilke & Todd, 2005; Penke, Todd, Fasolo & Lenton, in press). Characterizing how different psychological aspects of sociosexuality relate to the mating tactics that people show might tell us where to look for underlying psychological mechanisms and might thus aid their discovery in future research.

Table 1 about here

Three Components of Global Sociosexual Orientations: Behavior, Attitude, and Desire

According to Kinsey, individual differences in sociosexuality are first of all behavioral: some people have uncommitted sex on a regular base, others only seldom or never. Histories of more or less unrestricted sociosexual behaviors, in turn, are the developmental outcome of individual desires in transaction with personal and external (social and non-social) constraints on each individual's ability to fulfill his or her sociosexual desire.

Sociosexual desire can be defined as a specific form of interpersonal sexual desire (as opposed to the impersonal sexual desire that may motivate masturbation; Spector et al., 1996). Like general sexual desire (Beck et al., 1991; Ostovich & Sabini, 2004), sociosexual desire is an affective state that is characterized by sexual arousal, heightened sexual interest, and sexual fantasies. But unlike general sexual desire, unrestricted sociosexual desire comes with a sexual attraction that is specifically targeted at potential mates to whom no committed romantic relationship exists (see Simpson & Gangestad, 1991; Simpson et al., 2004). This preference for a certain class of incentives (i.e., uncommitted sexual partners) gives sociosexual desire a clear motivational component that makes it more concrete than the somewhat vague concept of general sexual desire (Bancroft, 1989). The affective state of passionate love (also called infatuation or "limerence") usually focuses sexual attraction on a single person and thus makes sociosexual desire highly restrictive (Fisher, 2004; Tennov, 1979). However, this highly activated state does not last forever, making sociosexual desires more unrestricted again after a period of time that has been said to be limited to approximately four years of romantic relationship (the "four-year-itch", Fisher, 1987). For

some, the infatuation period might be much shorter; these people tend to fall in and out of love quite frequently. As a consequence, they experience unrestricted sociosexual desire more often. Still others rarely or never fall into the state of infatuation (Tennov, 1979) – for them, the degree of sociosexual desire should be purely dispositional.

Sociosexual desire usually shows a sex difference: on average, men are much more willing to have sex with strangers (Clark & Hatfield, 1989; Buss & Schmitt, 1993; Schmitt et al., 2003), wish for a larger diversity of future sex partners (Buss & Schmitt, 1993; Schmitt et al., 2003), and have unrestricted fantasies more often (Ellis & Symons, 1990; Leitenberg & Henning, 1995). Indeed, these sex differences are among the largest ones found in psychology (Hyde, 2005). As a proximate explanation, it has been suggested that the physiological systems for sexual attraction are more dependent on the physiological systems for interpersonal attachment in women than in men (Diamond, 2003, 2004). Ultimately, *parental investment theory* argues that the sex difference in sociosexual desire is an evolved psychological adaptation to the inevitable differences in minimal parental investment between the sexes (Buss & Schmitt, 1993), which implies higher potential benefits and lower costs of short-term mating for men than for women (Trivers, 1972).

However, Gangestad and Simpson (2000) argued that intrasexual differences in sociosexual desires are much larger than intersexual differences. To account for intrasexual differences in sociosexuality, they proposed the *strategic pluralism model*. According to this model, men will be motivated to have multiple uncommitted sexual relationships due to their more unrestricted sociosexual desire, but their behavioral success will be limited by their ability to find willing sexual partners, because mating markets are competitive: As long as heterosexual men and women who desire different degrees of variety and commitment in their sexual relationships live in a population with roughly equal sex ratio, it will be impossible for every man and every woman to translate their sociosexual desire into behavior (Asendorpf & Penke, 2005; Penke et al., in press). There will always be women who fail to turn a sexual affair with the man they want into an exclusive long-term relationship, and most men won't have as many one-night-stands as they might wish for.

A man's behavioral success will depend on his ability to live up to the mate choice preferences of women. Female preferences, in turn, are contingent on the reproductive demand imposed by the environment: under harsh environmental conditions, when offspring survival is heavily dependent on biparental care, the model predicts that women will have restrictive sociosexual desires and prefer exclusive relationships with men who are good fathers and good providers. However, when environmental conditions are more luxurious, it is predicted that female desires will become less restricted. This should especially be the case when high prevalence rates of infectious diseases and parasites make mate choice for genetic benefits ("good genes" that are passed from the chosen mate to potential offspring)

highly important. Under such conditions, women might forego relationship exclusivity for mating opportunities with those few men with the best indicators of genetic quality (Simpson & Oriña, 2003). While it is likely that further conditions affect sociosexuality (e.g. Schmitt, 2005a), the principles of the strategic pluralism model nicely illustrate how personal and environmental factors constrain people's abilities to translate their sociosexual desires into behaviors.

Cultural values (like chastity or freedom of self-expression), traditions (like religious commandments), and institutions (like marriage systems) tend to reflect the reproductive demands of the environment, and can thereby reinforce the adaptive degree of sociosexuality in populations (Gangestad, Haselton & Buss, 2006; Low, 2007). Simultaneously, they provide powerful means to influence the sociosexuality of other people in the population. For example, Baumeister and Twenge (2002) argued that the cultural suppression of female sociosexual unrestrictiveness is likely the result of women constraining each others' behavior. This way, they can control the availability and consequently the exchange value of female sexual accessibility on the mating market (see also Baumeister & Vohs, 2004). Thus, the culturally expected degree of sociosexuality will not necessarily reflect the sociosexual desire or determine the sociosexual behavior of each particular individual, though it will likely influence each individual's sociosexual attitude and social self-presentation.

It follows that there are at least three distinguishable components of global sociosexual orientations: the individual degree of *desire* for uncommitted sexual relationships, the *attitude* towards sociosexuality that an individual acquired during socialization and communicates in social settings, and the sociosexual *behavior* that results from the individual desire and attitude in the socio-environmental context of a local mating market. These three components will have reciprocal effects on each other during an individual's lifelong development. For example, a young man might start with a highly unrestricted sociosexual desire during puberty, but may soon face the social disapproval of a restricted social environment (e.g. in his conservative hometown) and rejection by restricted women as a response to his unrestricted advances. This will put severe limits on his behavioral success with unrestricted mating tactics and might make his attitudes more restricted, but at the same time might have no effects on his desires. When he later changes to a more unrestricted environment (e.g. by moving to a more liberal city), he might encounter less restricted potential mates. At first, his learned restricted attitudes might inhibit his motivation to initiate unrestricted behaviors, but after a while his attitudes might change and reflect his unrestricted desire again. How well he is able to translate his desire into behavior will depend on his attractiveness. If his attractiveness is low, his continuing failures on the behavioral level might have a restricting impact on his attitude and maybe even his

desire. If his attractiveness is high, all three components may become very unrestricted - or he eventually falls in love (i.e., infatuation, limerence) and becomes highly restricted in his desire and actual behavior, but keeps some degree of unrestrictedness in his attitudes that reflect his unrestricted cultural environment.

Global sociosexuality, as measured by the SOI, provides a snapshot of this transactional process. It reflects the communality (shared core) of sociosexual desires, attitudes, and behavioral histories, which results from the correlations these interdependent components will naturally show at any point in time (see Simpson & Gangestad, 1991; Snyder, Gangestad & Simpson, 1986). While global sociosexual orientations are informative to a certain degree, each component has a very unique psychological meaning, and a more differentiated perspective might provide deeper insights into the construct of sociosexuality and human mating in general.

Overview

In the following, we aim to provide a more differentiated perspective on global sociosexuality by studying its three components separately, and their unique contributions to human mating. In Study 1, we revisited the structure of the SOI and revised it to become a multidimensional operationalization of the three sociosexuality components that we theoretically deduced: sociosexual behavior, attitude and desire. At the same time, we improved on some of the psychometric issues with the SOI that are frequently criticized (Asendorpf & Penke, 2005; Voracek, 2005; Webster & Bryan, in press). Furthermore, Study 1 investigated the relative strength of the relationships between sociosexuality components and a broad array of variables in the nomological network of global sociosexuality. Study 2 explores how the sociosexuality components differ in their temporal stability, developmental transactions with romantic relationships, degrees of assortative mating, and predictive validity with regard to flirting behavior when meeting an attractive stranger of the opposite sex, relationship outcomes, and number of future sexual partners.

Study 1

The purpose of Study 1 was to establish the three-component-structure of sociosexuality, in tandem with an appropriate measure. We first compared psychometric characteristics and sex differences in the well-established SOI with a revised version of the SOI that allows for a separate assessment of past sociosexual behavior, sociosexual attitudes, and sociosexual affectivity. Furthermore, we replicated parts of the nomological network that has been found for global sociosexuality (Simpson et al., 2004), including indicators of individual romantic relationship and sexual history, current relationship quality, general sexual desires, mate choice preferences, self-assessments, and related personality

traits and attitudes. For each correlate, we explored the unique contributions of each sociosexuality component.

Psychometric issues of the SOI. Despite its unquestionable success, various technical details of the SOI have been repeatedly criticized (Asendorpf & Penke, 2005; Voracek, 2005; Webster & Bryan, in press). These include the one-dimensional conceptualization of sociosexuality in the SOI, which is not only problematic on the theoretical grounds we outlined above, but also empirically: the internal consistency of the SOI tends to by quite variable across samples, sometimes falling below the threshold of what is usually regarded as acceptable. For example, across the 48 samples of the International Sexuality Description Project, Cronbach's α for the SOI (based on raw scores of all seven items) varied between .31 and .86 (Schmitt, 2005a). Furthermore, Webster and Bryan (in press) failed to find support for a one-factorial structure of the SOI in a large sample of college students. They suggested two correlated factors, sociosexual behavior and attitude, instead. However, these two factors also failed to provide a clear solution, since the behavioral expectancy item (number 2) showed equal loadings on both factors, and the fantasy item (number 4) was not well represented in this structure.

In addition to construct heterogeneity, the psychometric quality of the SOI is attenuated by the open response formats of the first three (behavioral) items. Such open questions for numbers of sexual partners tend to provide heavily skewed data, with low reliability of the values in the right tail of the distribution due to exaggerations, ballpark estimations, and systematic memory biases (Brown & Sinclair, 1999; Wiedermann, 1997). As a consequence, the first three items can contribute an amount of variance to the SOI total score that is several times higher than the variance of the other four items - one very high value can thus completely dominate an individual's total score. High values in the open SOI items often receive some form of special treatment, but there is no consensus on this among researchers: some trim only item 2 (e.g. Simpson & Gangestad, 1991), others trim all three open items (e.g. Webster & Bryan, in press), eliminate the upper 1% of the data (e.g. Schmitt, 2005a), or log-transform them to normality (Penke, Eichstaedt & Asendorpf, 2006). Most often, however, the way this problem is treated is not reported. Needless to say, this reduces the comparability of results.

Another factor that limits result comparability is that there is also no consensus in the literature with regard to the scoring of the SOI. This issue stems from the fact that the seven SOI items come with three different response scales of unequal length. As a consequence, the SOI items cannot simply be summed or averaged to a total score, but must be transformed to a common metric first. Simpson and Gangestad (1991) suggested three alternative ways to do so (factor analysis, *z*-standardization, and a weighting formula). One

of the latter two is usually used, even though they tend to provide different results (Voracek, 2005).

Finally, the origin of the SOI in the study of romantic couples (Simpson, 1987; Simpson & Gangestad, 1991) left its marks in the formulation of the fantasy item 4. In its original wording, only subjects who are currently involved in a romantic relationship are able to give a meaningful response. Since then, however, the SOI has been used in samples that included singles, with the consequence that item 4 is often skipped by these participants or omitted by the researchers (e.g. Clark, 2004, 2006; Brennan & Shaver, 1995; Greilling & Buss, 2000). Others (e.g. Schmitt, 2005a) circumvent this problem by changing the item text, even though the consequences for the construct validity are largely unknown.

The nomological network of global sociosexuality. Since sociosexuality is defined as the willingness to engage in uncommitted sexuality, its most obvious correlates are the desire for sexual variety (Schmitt, 2005a, b) and the lifetime number of sexual partners (Simpson & Gangestad, 1991; Ostovich & Sabini, 2004). However, as Simpson and colleagues (Simpson & Gangestad, 1991; Simpson et al., 2004) emphasized, an unrestrictive sociosexual orientation does not imply the general avoidance of long-term romantic relationships. Therefore, sociosexuality should only show weak relations to romantic attachment style. Instead, unrestricted individuals in committed relationships might consider having uncommitted sex with extra-pair partners (i.e., sexual affairs). More central to the construct of sociosexuality is a trade-off in the allocation of efforts (in terms of time, energy, money, and other limited resources) to either one primary mate or many mates: while restricted individuals tend to allocate their mating efforts in favor of the former, unrestricted individuals will prefer the latter option. It is thus not the mere engagement in long-term relationships that marks different sociosexual orientations, but the quality of these relationships (Simpson & Gangestad, 1991; Ellis, 1998).

Partly because unrestricted individuals care less about long-term relationships, partly because the social values and norms in Western societies do not tolerate “open relationships”, the lack of motivation for relationship exclusivity in unrestricted individuals presents a permanent threat for relationship stability (Simpson, 1987). A natural side-effect of unrestricted sociosexuality is thus an accumulation of ex-partners. Furthermore, since romantic commitment is encouraged in every major religion, sociosexual orientations tend to be more restrictive in more religious individuals (Kinsey et al., 1948, 1953; Laumann et al., 1994; Rowatt & Schmitt, 2003).

Gangestad and Simpson (1991) originally introduced the construct of sociosexuality as independent of general sexual desire. Indeed, they showed that it was unrelated to the frequency of sexual intercourse in couples. However, Ostovich and Sabini (2004) later pointed out that general sexual desire should reflect the overall sexual outlet, which is

arguably better captured by more impersonal indices, like masturbation frequency (see also Kinsey et al., 1948, 1953). When operationalized this way, there is a substantial relationship between general sexual desire and sociosexuality.

Sociosexuality is also related to mate choice, but in a highly specific manner. Several studies have shown that unrestricted individuals have a higher preference for physical attractiveness and other indicators of good overall condition (e.g. Gangestad & Simpson, 1992; Fletcher et al., 1999), with the theoretical rational that these traits signal good genetic quality (Simpson & Oriña, 2003; Penke et al., in press). In contrast, sociosexuality tends to be unrelated to other mate preferences (e.g. for warmth, reliability, or status). Since attractive individuals are more likely to be chosen as short-term mates, people seem to infer their own mate value from their sociosexual history and use this information for their mating decisions (Penke et al., in press; Landolt, Lalumiere & Quinsey, 1995; Clark, 2004, 2006).

Finally, a number of studies have related sociosexuality to various personality traits, with the overall result that unrestricted individuals tend to be extraverted sensation-seekers, while restricted people tend to be agreeable and inhibited (reviewed in Simpson et al., 2004).

Method

Sample. Study 1 is based on data from a large online survey. Despite former preconceptions, evidence is accumulating that online studies can provide valid psychological data (Gosling, Vazire, Srivastava, & John, 2004; Nosek, Banaji, & Greenwald, 2002), including data for sex research (Mustanski, 2001; Penke, Eichstaedt & Asendorpf, 2006). Online studies tend to provide heterogeneous and quite representative samples (Gosling et al., 2004), especially when compared to student samples. The current study was implemented in line with the guidelines for internet research proposed by Michalak and Szabo (1998) and the recommendations given by Kraut, Olson, Banaji, Bruckman, Cohen, and Couper (2004). It was limited to adult participants aged 18-50 years who reported heterosexual orientation and prior sexual experience. A total of 1,708 German-speaking internet users (1,026 men, 1,682 women, M = 24.2, SD = 7.1, Mdn = 22) completed the survey and agreed to a final item that asked if all there responses had been serious. The majority (92.8%) were native speakers. Slightly more than two thirds of the sample (71.3%) had at least a German Fachabitur or Abitur (college entrance examinations), while the others had left school with ten years of formal education or less. A total of 1,447 participants (53.4%) were currently involved in a committed romantic relationship. As an incentive, participants received an automatically generated personality profile after completing the study.

Measures. After a list of demographic questions, including items regarding age, sex, native language, education, religious affiliation, and degree of religiosity, the participants answered German adaptations of the following measures:

The *Self-Perceived Mate Value Scale* by Landolt, Lalumiere and Quinsey (1995) consists of eight items with 7-point rating scales that ask for the reactions one usually receives from members of the opposite sex (exemplary item: “Members of the opposite sex are attracted to me”; men: α = .91, *M* = 3.23, *SD* = 1.01; women: α = .93, *M* = 3.84, *SD* = 1.13).

A *questionnaire on romantic relationships and sexuality* included the original SOI (Table 1, for descriptive and psychometric statistics see Table 2), the five new sociosexuality items of the revised Sociosexual Orientation Inventory (SOI-R, see below and Appendix), and items asking for (1) current romantic relationship involvement, (2) the number of past romantic relationships that lasted longer than one month, (3) the total number of sexual intercourse partners so far, (4) the number of sexual intercourse partners while in a relationship with someone else (i.e., extra-pair copulation partners), and (5) their average monthly masturbation frequency. For all following analyses, the total number of sexual partners and the number of extra-pair copulation partners were log-transformed to reduce their skewness.

Those participants who reported current involvement in a romantic relationship also reported the duration of their current relationship and their average monthly sexual intercourse frequency with their partner. Furthermore, they answered the following questions on a dichotomous yes-no scale: “Do you believe your current partner is ‘Mr./Mrs. Right’?”, “Have you ever had a sexual affair with someone else while in the relationship with your current partner?”, and “Could you imagine having a sexual affair with someone else while being in the relationship with your current partner?”.

Finally, the participants who were currently in a relationship completed two questionnaires concerning their current relationship. The *Personal Relationship Quality Components* questionnaire (Fletcher, Simpson & Thomas, 2000) assesses six components of romantic relationship quality: satisfaction, commitment, closeness, trust, passion, and love. In this study, the short version of the questionnaire was used, which assesses each component with one item, all presented with a 7-point rating scales. In our analyses, we concentrated on the more reliable sum score (men: α = .86, *M* = 32.30, *SD* = 6.74; women: α = .87, *M* = 33.21, *SD* = 6.90), which can be regarded as a broad measure of relationship quality.

The *Relationship Questionnaire* (RQ, Bartholomew & Horowitz, 1991; German version by Doll et al., 1995) is a short measure of adult attachment. It encompasses short paragraphs describing each of the following attachment styles: secure, anxious, preoccupied,

and dismissive. Participants rated how well each description matched their own thoughts and feelings on 7-point rating scales. While attachment styles are often assessed as traits, there is a discussion in the literature how relationship-specific adult attachment styles are (Lehnart & Neyer, 2006). In this study, the instruction made clear that the descriptions refer to attachment to the current romantic relationship partner. It is thus used as a measure of relationship-specific attachment to the current mate. Besides analyzing the four attachment styles separately, we also followed Bartholomew and Horowitz (1991) and calculated two scores reflecting the "model of self" and "model of others".

In addition, one subgroup of the total sample (*N* = 867) indicated on 10-point percentile scales (as used by Swann, de la Ronde & Hixon, 1994) how much they preferred the following 20 characteristics in a potential mate: friendliness, dominance, creativity, physical attractiveness, even temper, responsibility, intelligence, sense of humor, athletic ability, parental qualities, good education, sex-appeal, good vocational prospect, sexual experience, fidelity, social status, richness, interesting personality, desire for children. We reduced this list of preferences by submitting the data to a principal component factor analysis.[1] Both the scree plot and a parallel analysis of 100 random datasets suggested the extraction of three factors (explained variance: 46.35%). After VARIMAX rotation, factor 1 was marked by friendliness (.74), fidelity (.73), and responsibility (.71). This factor closely resembles the warmth-trustworthiness ideal that was found by Fletcher, Simpson, Thomas and Giles (1999) in a more comprehensive analysis of partner ideals and the *attachment preference* that Penke et al. (in press) proposed based on a theoretical review. Richness (.78), social status (.75), and good vocational prospect (.71) were the items with highest loading on factor 2, a factor matching well to Fletcher et al.'s (1999) status-resources ideal and Penke et al.'s (in press) *resource preference*. Finally, factor 3 was marked by physical attractiveness (.65), sex-appeal (.64), interesting personality (.57), and creativity (.56), fitting with Fletcher et al.'s (1999) vitality-attractiveness ideal and Penke et al.'s (in press) *condition preference*. The factor structure of self-reported mate preferences in our study thus reflected three major preference dimensions that have been established in the mate choice literature. Individual factor scores were calculated for each participant.

A different subgroup of participants (*N* = 1,131) completed four other questionnaires instead. The *Short-Term Mating Index* (*STMI*) is based on three measures first introduced by Buss and Schmitt (1993): the "Time Known" measures, asking for the willingness to engage in sexual activity with an attractive stranger after various time intervals (6-point rating scales),

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[1] The reported results are based on the combined sample of men and women. Separate factor analyses for men and women resulted in an almost identical factor structure (Tucker's φ = .96, .95, and .92 for the attachment, resources, and condition preference factors, respectively). All results remained virtually unchanged when based on sex-specific factor scores.

the “Number of Partners” measure, asking for the number of desired sexual partners across various future time periods (open response format), and a single item with 7-point rating scale asking how actively one is currently seeking a short-term mate (e.g. a brief affair). Schmitt (2005b) aggregated three “Time Known”-items (1 month, 1 year, 5 years), three “Number of Partners”-items (1 month, 1 year, 5 years), and the short-term mate seeking item after *z*-standardization to the STMI, an index of overall short-term mating tendency. The participants in our study responded to a slightly different selection of five items from the same measures, namely the “Time Known”-item with an interval of 1 evening, the “Number of Partners”-items with periods of 1 year, 5 years, and the rest of one’s lifetime, and the short-term mate seeking item. We calculated an alternative STMI by summing these five items after log-transformation of the three (heavily-skewed) “Number of Partner”-items and sex-specific *z*-standardization of all five items. Despite being based on fewer items, our alternative STMI tended to be more internally consistent (α = .84 for both men and women) than the original STMI was in Schmitt’s (2005b) study (α = .79).

The *Sensation Seeking Scale* (form V by Zuckermann, Eysenck & Eysenck, 1978; German adaptation by Beaducel, Strobel & Brocke, 2003) is a 40-item questionnaire that assesses the individual tendency to seek out various, new, complex, and intensive experiences, even if this entails taking risks. Items are presented as pairs of opposing statements, of which participants have to choose the one they agree with more (dichotomous response format). In the current sample, the scale was reliable for both men (α = .78, *M* = 22.92, *SD* = 6.05) and women (α = .77, *M* = 20.87, *SD* = 5.80).

Trait social inhibitedness was measured with the *Shyness Scale* by Asendorpf and Wilpers (1998), which consists of five items with 5-point rating scales (exemplary item: “I feel shy in the presence of others”; men: α = .83, *M* = 13.92, *SD* = 4.10; women: α = .83, *M* = 13.36, *SD* = 4.03).

The *Sex Drive Questionnaire* by Ostovich and Sabini (2004) is a self-report measure of what Kinsey et al. (1948) termed “total sexual outlet”. It reflects the individual degree of sexual activity, be it with a partners or alone. It consists of four items with varying response formats (e.g. “How often do you orgasm in the average month?”), which are aggregated after *z*-standardization. The internal consistency for this scale was marginally acceptable (α = .68 for men and .72 for women).

Results

The structure of the SOI. The SOI was originally proposed by Simpson and Gangestad (1991) as a one-dimensional measure of a broad construct. We tested this assumption in a confirmatory factor analysis of a model that had all seven SOI items (which were *z*-standardized prior to the analysis) loading on the same latent factor. As already found

by Webster and Bryan (in press), this model fitted the data poorly ($\chi^2_{(14)}$ = 992.18, p < .001, *CFI* = .815, *NFI* = .813, *SRMR* = .101). Next, we attempted to replicate the two-factor structure of the SOI advocated by Webster and Bryan, with items 1, 2 and 3 loading on a "behavior" factor, and items 2 and 4 to 7 loading on an "attitude" factor that is correlated with the behavior factor. Just as in their study, this model fitted our data well ($\chi^2_{(12)}$ = 40.53, p < .001, *CFI* = .995, *NFI* = .992, *SRMR* = .019), and significantly better, not only as the one-factor model ($\Delta\chi^2_{(2)}$ = 475.83, p < .001), but also as two similar two-factor models that restricted item 2 (which asks for expected future sex partners) to load exclusively on either the behavior ($\Delta\chi^2_{(1)}$ = 526.23, p < .001) or the attitude factor ($\Delta\chi^2_{(1)}$ = 16.62, p < .001). The current data thus fully confirms the results reported by Webster and Bryan.

However, we also tested an additional model, which modified the Webster-and-Bryan model toward a three-factor structure. The modification was that item 4 (which asks for extra-pair sexual fantasies) did not load on the attitude factor any more, but defined a distinct "desire" factor. This third factor was correlated with both the attitudinal and the behavioral factor on the latent level. Our alternative three-factor model showed a good fit to the data, almost identical to the Webster-and-Bryan model ($\chi^2_{(12)}$ = 42.11, p < .001, *CFI* = .994, *NFI* = .992, *SRMR* = .019), had the same number of degrees of freedom, and an only slightly worse *AIC* (48,431.32 vs. 48,429.74 for the Webster-and-Bryan model). On empirical grounds, these two models can thus be regarded equally plausible.

We assume that there is a straightforward reason why the three-factor structure of sociosexuality, which we favor on theoretical grounds, did not turn out to be superior to the two-factor model: the affective component of sociosexuality is not well represented in the items of the SOI (i.e., only in item 4, which has the psychometric flaws discussed above). In addition, both Webster and Bryan's (in press) and our results underlined the ambiguous nature of the expectancy item 2, which showed simultaneous affinities to both behavioral and attitudinal sociosexuality.

Table 2 about here

The revised Sociosexual Orientation Inventory (SOI-R). Because of the structural and psychometric issues of the SOI, we added five new sociosexuality items to the questionnaire battery of the current study, which have been selected from a total pool of 40 items in a series of pilot studies (details are available from the first author.) These five items were used to construct a psychometrically improved revision of the SOI, the SOI-R.

One item ("In your entire lifetime, with how many different people have you had sexual intercourse without having an interest in a long-term committed relationship with this person?", number 3 in the Appendix) was intended as a replacement for the ambiguous item 2 of the SOI. Together with items 1 and 3 of the SOI, these three items were chosen to reflect the behavioral component of sociosexuality (facet "*Behavior*"). To avoid the issues

that come with the open response format of these items in the SOI, we recoded the open responses to nine categories. These nine categories may be used to form a 9-point rating scale for these items in future studies (see Appendix).

The attitudinal component of sociosexuality is already well reflected in items 5 to 7 of the SOI. However, the text of SOI item 7 is very long and complicated, which might lead to measurement problems with less attentive or less educated subjects. We thus replaced it with a shorter alternative ("I do *not* want to have sex with a person until I am sure that we will have a long-term, serious relationship."). Together with the original items 5 and 7, it forms the facet "*Attitude*".

Finally, three of the novel items (items 7 to 9 in the Appendix, e.g. "In everyday life, how often do you have spontaneous fantasies about having sex with someone you have just met?") reflected aspects of the sociosexuality facet "*Desire*". Note that all new Desire items avoid the requirement of an existing romantic relationship. Since this is not the case for SOI item 4, we dropped it in the revised version. Note also that the rating scales of the SOI-R items now have nine alternatives, while SOI item 4 had eight. This way, the number of response alternatives is the same for all nine SOI-R items.

The SOI-R thus contains a total of nine items, four taken from the SOI and five new ones. The structure of the SOI-R was also evaluated with confirmatory factor analyses. As with the SOI, we first tested a one-dimensional model, with all nine items loading on a single factor. This model was not supported by the data ($\chi^2_{(27)} = 6582.64$, $p < .001$, *CFI* = .503, *NFI* = .503, *SRMR* = .173). Next, we tested a model with a behavioral (SOI-R items 1 to 3) and a correlated "broad-sense-attitudinal" factor (SOI-R items 4 to 9), corresponding to the two-factor Webster-and-Bryan model. Again, the fit was poor ($\chi^2_{(26)} = 3465.62$, $p < .001$, *CFI* = .739, *NFI* = .738, *SRMR* = .160). In contrast, the model we theoretically expected, with three correlated factors ("Behavior", "Attitude", and "Desire"), each defined by three items (see Figure 1), fitted the data well ($\chi^2_{(24)} = 224.69$, $p < .001$, *CFI* = .985, *NFI* = .983, *SRMR* = .035), significantly better than the one-factor ($\Delta\chi^2_{(3)} = 2119.32$, $p < .001$) and the two-factor model ($\Delta\chi^2_{(2)} = 1620.47$, $p < .001$).

We also tested for sex differences in the SOI-R structure by fitting the three-factor model separately to data from men and women and then constraining all factor loadings and correlations to be equal across sexes. This model provided a good fit to the data ($\chi^2_{(57)} = 273.43$, $p < .001$, *CFI* = .983, *NFI* = .978, *SRMR* = .045), though the fit improved somewhat when the latent correlation between sociosexual Behavior and Attitude was allowed to differ between men and women ($\Delta\chi^2_{(1)} = 5.29$, $p < .05$). Since this sex difference was also found by Webster and Bryan (in press) for the SOI, we report this correlation separately for both sexes in Figure 1.

The three items that correspond to each of the three SOI-R components yield very reliable sociosexuality facet scales (Table 2), especially when taking their briefness into account. The SOI total score corresponds especially well to the SOI-R Behavior facet (r = .77), even better than the average of the three SOI behavioral items (items 1-3, α = .67) (r = .70), which differs only in one item and the scale format. Not surprisingly, the SOI-R attitude facet corresponds almost perfectly to an aggregate of the SOI's three attitudinal items (α = .83, r = .94), two of which also contribute to the SOI-R facet. More interestingly, the SOI-R Desire facet corresponds very well to the fantasy item 4 of the SOI (r = .64), even though there is no item overlap here.

The positive intercorrelations of the SOI-R facets (Figure 1) allow for aggregating all nine SOI-R items to a global sociosexuality index, similar to the one provided by the SOI. This aggregate also shows good reliability (Table 2). The correspondence of the SOI and SOI-R total scores is not exceptionally high (r = .64 for men and .68 for women), likely due to the different emphasis both scales put on the different sociosexuality components.

Figure 1 about here

Sex differences. As can be seen in Table 2, the well-established sex difference for the SOI was replicated in this sample (Cohen's d = .27) and was even more pronounced for the SOI-R total score (d = .61). However, analyses on the level of the SOI-R facets indicated that the Behavior facet did not contribute to the sex differences (d = .06). In contrast, the Attitude facet showed a sex difference comparable to the one found for global sociosexual orientations (d = .43), while the Desire facet showed a much larger sex difference (d = .86), which is large compared to conventional standards (Cohen, 1969). A two-way mixed ANOVA with the three facets as within-subject factor and sex as between-subject factor yielded a significant interaction ($F_{(2,\ 5412)}$ = 137.00, p < .001, η_p^2 = .05), indicating that the facet differences in the sex differences were statistically significant. Pairwise comparisons confirmed that this is true for all facet combinations (ps < .001).

Effects of relationship status and duration. We first tested for effects of the current romantic relationship status on global sociosexuality in two 2 (sex) x 2 (relationship status) univariate ANOVAs, with either the SOI or the SOI-R total score as dependent variable. While only sex had a significant effect on the SOI ($F_{(1,\ 2704)}$ = 44.97, p < .001, η_p^2 = .02), sex, relationship status, and their interaction had all significant effects on the SOI-R (all ps < .001, η_p^2 = .08, .01, and .004, respectively). Subsequent t-tests indicated that the SOI-R total score was significantly lower in coupled than in single women ($t_{(1680)}$ = 7.34, p < .001, d = .36), but men did not differ by relationship status ($t_{(1024)}$ = 1.51, p =.13, d = .09). In order to solve this discrepancy, we ran a 2 (sex) x 2 (relationship status) MANOVA with the three SOI-R facets as dependent variables. Here, the effect of sex was significant on the Attitude ($F_{(1,\ 2704)}$ = 113.54, p < .001, η_p^2 = .04) and the Desire facets ($F_{(1,\ 2704)}$ = 500.13, p < .001, η_p^2 = .16), but

not on the Behavior facet ($F_{(1, 2704)}$ = 2.84, p = .09, η_p^2 = .001). Relationship status had no effect on the Attitude facet (F < 1), but it had on Desire ($F_{(1, 2704)}$ = 344.26, p < .001, η_p^2 = .11) and slightly on Behavior ($F_{(1, 2704)}$ = 10.28, p = .001, η_p^2 = .004). Weak interactions between sex and relationship status were significant for the facets Attitude ($F_{(1, 2704)}$ = 7.81, p = .005, η_p^2 = .003) and Desire ($F_{(1, 2704)}$ = 13.45, p < .001, η_p^2 = .005). Subsequent t-tests indicated that individuals in a relationship showed a slightly more unrestricted behavior than singles ($t_{(2706)}$ = 3.00, p = .02, d = .12), and that men had a slightly more unrestricted attitude when in a relationship ($t_{(1024)}$ = 2.36, p = .02, d = .15), while relationship status had no effects on attitudes in women ($t_{(1680)}$ = 1.55, p < .12, d = -.08). More interestingly, individuals in a relationship had substantially more restricted desires ($t_{(2706)}$ = 19.10, p < .001, d = .73), though this effect was larger in women ($t_{(1680)}$ = 18.20, p < .001, d = .89) than in men ($t_{(1024)}$ = 9.29, p < .001, d = .58).

Within the subsample of individuals in a relationship, we also tested for effects of relationship duration on sociosexuality. Neither the SOI nor the SOI-R or any of its facets showed linear relationships with relationship duration (log-transformed to reduce skew) (all rs < |.10|, all ps > .05). However, interesting results emerged when we investigated the "four-year-itch"-hypothesis proposed by Fisher (1987). We compared those subjects who had been in a relationship for four years or less (N = 1,043) with those whose relationship already lasted for more than four years (N = 376). Two 2 (sex) x 2 (relationship duration) ANOVAs with either the SOI or the SOI-R total score as dependent variable yielded main effects of sex (SOI: $F_{(1, 1415)}$ = 43.77, p < .001, η_p^2 = .03; SOI-R: $F_{(1, 1415)}$ = 141.80, p < .001, η_p^2 = .09) and relationship duration (SOI: $F_{(1, 1415)}$ = 4.93, p = .03, η_p^2 = .003; SOI-R: $F_{(1, 1415)}$ = 5.39, p = .02, η_p^2 = .004), but no interaction effects (ps > .05), with those in a relationship for four years or longer being slightly more unrestricted (SOI: $t_{(1417)}$ = 2.32, p = .02, d = .13; SOI-R: $t_{(1417)}$ = 3.07, p = .002, d = .18). A 2 (sex) x 2 (relationship duration) MANOVA with the three SOI-R facets as dependent variables and subsequent t-tests indicated, beside the usual pattern of sex differences, that the two relationship duration groups differed only in their Desire ($F_{(1, 1415)}$ = 18.93, p < .001, η_p^2 = .01), but not in their Attitude or Behavior (ps > .10). All interaction effects were non-significant (ps > .10).

Both relationship status and relationship duration above or below Fisher's four-years-threshold thus had their most noteworthy effects on the Desire component of sociosexuality. These effects are illustrated in a slightly different manner in Figure 2. All sex and group differences in this figure are significant at p < .001.

Figure 2 about here

The nomological network of global sociosexuality and its components. In order to dissect the relations between global sociosexual orientations and its correlates, we first compared facet-level relationships with the SOI and SOI-R total scores. These zero-order

correlations are shown in the first five columns of Tables 3a and b. However, since the three facets also contain common variance that reflects their socio-developmental interdependences, the nomological network of their unique variance should give a clearer picture of the nature of their relationships with the correlates of global sociosexuality. We therefore calculated uniqueness scores for Behavior, Attitude, and Desire by simultaneously regressing each of the three facets on the other two facets. The regressions were run separately for men and women. The resulting residual scores reflect the variance of each facet that is not shared with the other two. The three rightmost columns of Tables 3a and b show the correlates of these three uniqueness scores (technically semi-partial correlations).[2]

Due to the threat of error accumulation that comes with such a large number of significance tests, we set the alpha to a more conservative level of .01. However, the very large sample size already ensures a high robustness of the results.

Tables 3a, b about here

As expected, both the SOI and the SOI-R total scores showed substantial correlations in both sexes with the total number of past romantic relationships, sexual partners, and extra-pair sexual partners, as well as, to a lesser degree, self-perceived mate value. The correlations of the three SOI-R facets with these variables indicate that all these relationships are mainly due to the Behavior facet. This conclusion is strongly supported by the uniqueness correlations: with the other two facets statistically controlled, only the unique variance of the Behavior component of sociosexuality relates to the quantity of prior relationships, sex partners, and sexual infidelities, and to self-perceived mate value.

For both sexes, the SOI-R total score (and in women also the SOI) showed a small, but significant correlation with religiosity and the self-reported condition preference, suggesting that unrestricted individuals tend to be less religious and prefer attractive, vital mates. Both indices of global sociosexuality also correlated negatively with self-reported attachment preference in women. In all these cases, however, the uniqueness correlations revealed that the effects are mainly driven by the Attitude components (though Desire has also a unique effect on the female condition preference).

[2] Note that uniqueness correlations provide a less biased estimate of the unique contribution of each facet than either beta coefficients from multiple regressions on all three facets, or correlations with component scores from a principal component analysis that rotated the facets to orthogonality. While both multiple regressions and principal component analyses divide contributions of the communalities (i.e., shared variances) of the facets to the relationships with other variables equally between the betas or correlation coefficients, shared variance effects are completely controlled in uniqueness correlations. Furthermore, uniqueness correlations circumvent potential multicollinearity issues. However, the general pattern of results in both Study 1 and 2 remained virtually unchanged when either multiple regressions or orthogonal components were used.

The desire for sexual variety (as assessed by the STMI), an obvious correlate of global sociosexuality, showed strong correlations with all SOI-R facets. Therefore, it is interesting that only the uniquenesses of the facets Attitude and Desire correlate with the STMI – genuine sociosexual behavior seems not to be represented in this measure. The Sensation Seeking Scale, on the other hand, apparently reflects a personality dimension that is truly related to all aspects of sociosexuality. The same is not true for shyness, which relates to sociosexual Behavior and Attitude, but not to Desire.

Sexual desire within a relationship, as indexed by the sexual intercourse frequency with the current partner, shows only very weak relations to sociosexuality and its components. In contrast, general sexual desire, as indexed by the Sex Drive Questionnaire and the masturbation frequency, shows substantial relationships with sociosexuality, especially with sociosexual Desire. The current study was thus able to simultaneously replicate the findings of Simpson and Gangestad (1991) and Ostovich and Sabini (2004).

Substantial negative relations were found between unrestricted sociosexuality and indicators of relationship quality, commitment, and exclusivity in both men and women. What all these variables have in common is that they overlap with the unique sociosexual Desire variance. The only incremental contributions of other sociosexuality components are that considering being unfaithful to one's current partner correlates with the Attitude component, while having already been unfaithful in the current relationship correlates with the Behavior component.

In addition to sexual intercourse frequency, further evidence for the discriminant validity of the SOI and SOI-R is provided by the very weak relationships between aspects of sociosexuality and romantic attachment styles. At best, the relationships between unrestricted sociosexuality (especially the Desire component) and fearful and dismissive attachment styles, as well as a negative model of others, are noteworthy.

Age effects. Both the SOI (men: $r = .17$, $p < .001$; women: $r = .12$, $p < .001$) and the SOI-R (men: $r = .09$, $p = .006$; women: $r = .07$, $p = .003$) total scores were weakly correlated with age. On facet level, Behavior increased with age ($r = .25$, $p < .001$ for both sexes, possibly reflecting the natural accumulation of partners over the lifespan or cohort effects), while Attitude was unaffected, and Desire showed a weak decline in women ($r = -.13$, $p < .001$). This pattern was replicated in the uniqueness correlations. To control for potential confounding effects of age, we reran all (M)ANOVAs with age as a covariate. Only the weak effect of relationship status on Behavior and the effects of relationship duration on the SOI and SOI-R total scores were not replicated. Furthermore, the reported pattern of correlations in the nomological network remained virtually unchanged when age was partialled out.

Discussion

Study 1 strongly supported our initial contention that global sociosexuality is not a unitary construct, but has different components that make unique contributions to the understanding of sociosexual orientations. Like Webster and Bryan (in press), we were unable to confirm the one-dimensional structure of the SOI. Instead, we could replicate the two-factor structure they suggested, but also showed that a model with the three factors we expected theoretically (Behavior, Attitude, and Desire) fitted our data just as well. The three-factor structure of sociosexuality received even stronger support when tested in our revised version of the SOI, where the Desire component was adequately represented by more than one item.

We were able to replicate the nomological network of the SOI with the SOI-R. However, an analysis of the three SOI-R facets revealed that (1) sex differences are most pronounced in sociosexual Desire, while absent in the Behavior component, (2) relationship status and duration (Fisher's "four-year-itch") have their strongest effects on Desire, and (3) many correlates of sociosexuality are specific to only one of the three components (especially when their shared variance is controlled). These results confirm the SOI-R as a valid measure of sociosexuality, and support the three distinguishable sociosexuality components we hypothesized on theoretical grounds. However, Study 1 is based solely on cross-sectional data. From these concurrently assessed self-reports, we cannot evaluate the usefulness of differentiating the three proposed sociosexuality facets in the prediction of future mating behavior and relationship outcomes. Furthermore, we cannot tell from individual data what dyadic effects sociosexuality has within romantic relationships, or if they show different developmental patterns or degrees of assortative mating. Study 2 was aimed to answer these additional questions.

Study 2

In Study 2, we assessed the predictive validity of sociosexual Behavior, Attitude and Desire compared to the global sociosexual orientation with regard to three criteria: (1) flirtatious behavior during an interaction with an attractive opposite-stranger, (2) stability and change of romantic relationship status (single vs. in a relationship) over a one-year-period, and (3) the degree of sexual promiscuity over the same time interval. In order to analyze dyadic effects of sociosexuality, we assessed participants currently involved in a romantic relationship together with their partners. Finally, we utilized this data to explored assortative mating for and the temporal stability of sociosexuality on global and facet levels.

Method

Sample. Participants were recruited for a study on "Love, Sexuality, and Personality" by advertisements in various public places and a diverse range of media. They signed up for the study by answering a pre-questionnaire on the internet. An honorarium of 16 € (about 21

$) and personal feedback were offered as an incentive. Registration required providing demographic and relationship information that was used to pre-screen participants for current relationship-, marriage-, and parental status, age, sexual and relationship experience, sexual orientation, and current psychoactive medication.

A final sample of 283 heterosexual, sexually experienced participants without children, aged 20-30 years (*M* = 23.7 years, *SD* = 2.7; 140 males, 143 females) completed all tasks. They consisted of 70 unmarried couples and 143 singles. All participants had been in at least one committed relationship for at least one month, with a mean of 3.5 relationships (*SD* = 2.3). The couples were together for 0.67 to 7.96 years, with a mean of 2.74 years (*SD* = 1.63). All participants were native speakers and were not on psychoactive medication in the three months prior to the study. Sixty percent were currently students, while 15.7% had left school with ten years of formal education or less (i.e., no German Abitur or Fachabitur).

Procedure. After completing the online pre-questionnaire, suitable participants were scheduled for a 2-hour lab session. All participants were tested individually, guided by a same-sex experimenter. Couples arrived at the laboratory together, but were tested separately in parallel sessions. While in the lab, participants completed various assessments, including filling out the SOI and the SOI-R (see Table 1 for descriptives and reliabilities), as well as a videotaped dyadic get-acquainted interaction with an opposite-sex confederate who was introduced as another participant of the study (Ickes, 1983; Ickes, Bissonnette, Garcia & Stinson, 1990). Standardized photographs were also taken. At the end, participants were debriefed, asked to provide their email and phone numbers for a follow-up study, and received payment and a personality profile. One year after the lab session, the follow-up was conducted as an online study.

Interaction with confederate. Two female and three male students served as conversation partners for the participants during the interaction. These confederates were carefully chosen for communicative skills, above-average attractiveness, heterosexual orientation, appropriate age, and an overall appearance comparable to the other confederate(s) of the same sex. Confederates were instructed to act like they were single and participating in the study, naïve to the situation. They were trained to be friendly and open at the beginning of the interaction, and to adjust their behavior to the behavior of their current interaction partner, such that the course of the interactions was largely determined by the participants. No participant had ever met his or her confederate before.

When the participant had completed the first assessments, the experimenter guided the participant to another room that looked more like a living room than a typical laboratory space, and offered one of two chairs to the participant. The chairs were arranged next to a small table such that the conversation partners were sitting in a 120 degree angle to each other. Each conversation partner was focused by a video camera at the opposite side of the

room that captured a close-up view of the face from a close-to-frontal angle (only the camera focusing the participant was actually recording the conversation, the other served as a dummy to support the cover story). A third camera recorded both conversation partners from a 120 degree angle.

As part of the cover story, the experimenter made recordings of the participant's voice (unrelated to the present study), which were introduced as an intermission to bridge the waiting time for the conversation partner. Afterwards, the experimenter re-entered the room with one of the opposite-sex confederates, offered him or her the other seat, and briefly introduced him or her as another participant of the study. Subsequently, the experimenter explained that the purpose of the setting was to study what happens in the first minutes when strangers meet, asked both the participant and the confederate to get to know each other for ten minutes, explained that the conversation will be video-recorded, and left the room. Seven minutes later (not ten, as announced), the experimenter re-entered the room and separated the participant and the confederate for the rest of the study. No participant showed serious signs of doubt about the cover story, an impression that was confirmed by unobtrusive inquiries by the experimenters at the end of the study. After the debriefing, all subsequent reactions of the participants were positive towards the study, with no sign of harm due to the deception.

Confederate ratings. The confederate rated the participants directly after the conversation on various items, including "Would you give this person your phone number?" and "Would you go out to the cinema with this person if he/she asked you?", both taken from Grammer (1995) and rated on a scale from 1 ("no way") to 5 ("I would love to"). Since these two variables were highly correlated (r = .73 for the male and .70 for the female confederates' ratings, both ps < .001), they were averaged to a single score labeled "Interest of Confederate".

Follow-up. Exactly 360 days after taking part in the lab session (t1), participants received an email that offered them a free cinema ticket for responding to a 20-minute follow-up online-questionnaire (t2). Non-responders received a reminder email ten days later and were called by one of the experimenters from the lab study after 14 days. The questionnaire first asked for changes in romantic relationship status over the past twelve months, with two response alternatives ("currently single" and "currently in a relationship") for those who were single at t1, and four alternatives ("in the same relationship all the time", "in the same relationship, but separated in between", "in a different relationship", and "currently single") for individuals who were in a relationship at t1. Subsequent questions included the SOI, the SOI-R, an open item asking for the number of partners with whom they have had sex for the first time during the last twelve months, and various items unrelated to the present study.

Video analyses: global ratings. Four independent, trained raters (two women, two men) rated the flirting behavior of the participants within the first three minutes of the videotaped interaction twice. In a first round, they rated all interactions recorded from the side perspective (with both interaction partners completely visible). In a second round, ratings were done based on the frontal facial recordings. Thereby, both gross body positions and movements of both conversation partners and more subtle facial expressions of the participant were captured in the ratings. In both rounds, videos were presented with audio. All ratings were done every 30 seconds (indicated by a timed acoustic signal) on a scale from 1 (*not very much) to 7 (very much)* and labeled *"*How much does this person flirt with the confederate?*"*. Thus, each rater provided a total of 12 ratings for each participant. All raters were unacquainted with the participants and blind to their relationship status and the results of all other parts of the study.

For both rating rounds, the interrater agreement was high for each of the six 30-second-segments (side perspective: α = .84 to .88, frontal perspective: α = .85 to .90). Thus, ratings of all four raters were aggregated for each segment. Within each perspective, the six aggregated segment ratings were further aggregated to highly reliable composites (α = .98 and .97 for the side and frontal perspective, respectively). Since these two composite flirting ratings were highly correlated (*r* = .69), they were aggregated to a final *Global Flirting Rating* composite, based on 2 (camera perspectives) x 6 (30-second-segments) x 4 (raters) = 48 ratings per subject. Potential influences of the specific confederate a subject faced during the conversation were statistically controlled by regressing the Global Flirting Rating on the dummy-coded confederates within sexes and using the residuals in all analyses.

Video analyses: behavior codings. The videos of the interaction were used to code 16 objective behaviors of the participants within the first three minutes, including the duration of (1) gazing at the confederate's face, (2) speaking, (3) smiling, (4) laughing, (5) illustrators (communicative gestures), and adaptors (non-illustrative hand movements) to the (6) body, (7) face, and (8) other objects (mostly the chair or table), as well as the frequency of (9) short glances (lasting less than one second) towards the confederate, (10) "look throughs" (passing looks at the confederate without fixation), (11) interactive gestures, (12) hair flips or tosses, (13) "coy smiles" (smiles towards the confederate, followed by an immediate downward gaze), (14) "head akimbos" (folding of the hand behind the head, thereby exposing the axillaries), (15) "backchannel responses" (affirmative nods or vocalizations), and (16) touching the confederate (except handshakes). In addition, the speaking time of the confederate was coded. The speaking time of both the participant and the confederate were subtracted from the total time coded (three minutes) to arrive at the duration of silence in each conversation. All behaviors were chosen because they showed relations to contact-readiness, rapport and flirtation in earlier studies (Asendorpf, 1988; Bavelas, Chovil, Lawrie &

Wade, 1992; Bernieri, Gillis, Davis & Grahe, 1996; Eibl-Eibesfeldt, 1989; Grammer, 1995; Grammer, Kruck, Juette & Fink, 2000; Moore, 1985; Simpson, Gangestad & Biek, 1993).
Two trained research assistants coded the behaviors using The Observer 5.0 (Noldus, 2003). Twenty-one videos were double-coded to allow reliability determination. All behaviors involving hand or arm movements (e.g. illustrators, adaptors) were coded from the clips with full body shots from the side, while all other behaviors were coded from the frontal facial recordings. Head akimbos and touching the confederate did not occur in any of the conversations. Intercoder reliabilities (*ICC*s) for the other behaviors were high, ranging from .86 (backchannel responses) to .99 (facial gazing, short glances).

Facial attractiveness ratings. During the lab session, participants' faces were videotaped with a Cannon MV700i camcorder while they stood upright in front of a neutral background and maintained a neutral facial expression. Later on, video capturing software was used to choose the one frame with the most frontal and neutral recording of each participant's face and to convert it to a digital picture. Size was standardized to identical interpupilar distance. These pictures were divided into four sets of equal size (N = 70-71), two for male and two for female participants. Each of the four sets were rated by 15 different heterosexual undergraduate students of the opposite sex (age M = 24.4, SD = 6.7), who judged the attractiveness of each picture on a scale from 1 (not attractive at all) to 7 (very attractive) in exchange for course credit. Interrater reliabilities were good for both male (α = .90 for set 1 and .91 for set 2) and female (α = .91 for set 1 and .89 for set 2) raters, so that ratings could be aggregated across raters after z-standardization.

Results

Attrition analysis. For the online follow-up study, 91.2% (N = 258) of the lab sample provided information on their current relationship status, while 85.5% completed the whole follow-up questionnaire, including the SOI and the SOI-R. Both those who responded partly and those who responded completely had, on average, received higher education and were more unrestricted on the Behavior facet of the SOI-R than those who failed to do so (ps < .05), but did not differ significantly with regard to their age, sex, relationship status, scores on the SOI-R facets Attitude and Desire, the Global Flirting Rating, or rated facial attractiveness, all as assessed at t1.

Sex differences in sociosexuality. As in Study 1, sex differences were larger for the SOI-R than for the SOI, and largest for the Desire facet, medium for Attitude, and absent for Behavior (Table 2). Again, a two-way mixed ANOVA with the three facets as within-subject factor and sex as between-subject factor yielded a significant interaction ($F_{(2, 562)}$ = 8.46, p < .001, η_p^2 = .03), indicating significant facet differences in sex differences. However, pairwise comparisons revealed that only the sex differences between Behavior and the other two

facets were statistically significant in this sample (*p*s < .001; *p* = .28 for the Attitude-Desire difference in sex differences).

Prediction of flirting behavior. We tested how sociosexuality predicted flirting behavior in the lab, using the Global Flirting Rating as a criterion. Flirting with strangers is a proximate behavioral criterion for sociosexuality, since it entails the active courtship patterns that might initiate sexual contacts or new romantic relationships. As can be seen in Table 4, the SOI and SOI-R global scores predicted flirting behavior in both men and women, as does the Behavior facet of the SOI-R. In contrast, the Attitude facet is unrelated to the Global Flirting Rating in both sexes. Finally, the Desire facet is strongly predictive of the Global Flirting Rating in men, but only marginally in women. An interesting pattern emerged from the uniqueness correlations: while they confirmed the predictive value of past sociosexual Behavior and male sociosexual Desire, the unique variance of sociosexual Attitude turned out to be a *negative* predictor of the Global Flirting Rating for both men and women. It appears that people display flirting tendency towards attractive strangers in line with their sociosexual desires and behavioral histories, even if this contradicts their explicit attitudes.

Tables 4 and 5 about here

To have a closer look at how sociosexuality is communicated in get-acquainted situations, we analyzed the objectively coded behavior of the subjects during the conversation. In a first step, we reduced the 15 behaviors that actually occurred in our sample with sex-specific principal component factor analyses. A comparison of the eigenvalues with a parallel analysis of 100 random datasets with identical sample size suggested four factors for men and five for women, a decision that was further supported by an inspection of the scree plot.[3] Table 5 presents the factor solutions after orthogonal rotation, along with descriptive statistics. The first three factors were very similar in both sexes (Tucker's φ = .93, .93, and .86, respectively). Factor 1 was marked by facial gazing and few short glances, thereby reflecting how directly the participants looked at the confederates. We called this factor "Fixation". Factor 2 showed high positive loadings by speaking time and amount of illustrators used, and a negative loading by the amount of silence that occurred. We labeled it "Expressivity". Factor 3 was marked by the amount of smiling and laughing the participants showed, and was consequently called "Joyfulness". Factor 4 showed low congruence between the sexes (Tucker's φ = .24). However, for both sexes the highest loading behavior was the amount of body adaptors used by the subject. In addition, the factor was marked by coy smiles in men and by look throughs and interactive gestures in women. Since all these behaviors can be linked to social inhibition, we called the

[3] When a fifth factor was extracted for men, it turned out to be not interpretable, with no coded behavior loading .60 or higher.

factor “Inhibitedness” in both sexes (but marked the female factor with an apostrophe to indicate its sex-specific structure). Finally, the fifth factor, which we found only in women, was marked by hair flips/tosses and coy smiles, two prototypical female courtship behaviors, leading to the label “Flirting Gestures”.

The relationships between sociosexuality, the coded behavior factors, and the Global Flirting Rating were analyzed in Brunswikean lens models (Brunswik, 1956). In a lens model, the accuracy of the assessment of a latent trait (here sociosexuality) during the social perception of a person’s behavior (here the Global Flirting Rating) is explained by the validity of objectively observable cues (here the coded behavior factors and their relationship to sociosexuality) and the utilization of these cues by the perceivers (here the relationship between the behavior factors and the flirting rating) (see left half of Figure 3). For both men and women, we calculated separate lens models with the SOI and SOI-R total scores, each of the three SOI-R facets, and each facet’s uniqueness as the latent trait. The confederates were dummy-coded and statistically controlled. Note that within sex, the cue utilizations stay the same, no matter which sociosexuality score is used; they can be found in Figure 3. In contrast, the accuracies and cue validities depend on which latent trait (i.e., sociosexuality variable) is analyzed in the lens model; these are all reported in Table 4.

Figure 3 about here

As Table 4 shows, none of the four objective behavior factors were valid cues to the SOI or SOI-R total scores of men. Only an analysis on facet level revealed that high scores on the Fixation factor (and marginally the Expressivity factor) predicted male sociosexual Desire. These findings were corroborated with the uniqueness regressions, which also revealed a negative relationship between the Fixation factor and Attitude. In itself, unrestricted sociosexual Desire apparently leads men to more strongly fixate an attractive woman during a conversation, while an unrestricted explicit Attitude has the opposite effect. In women, both the SOI and the SOI-R total scores predicted more joyful behavior during the interaction, indicating that the amount of female smiling and laughing is a valid cue to global sociosexuality. On facet level, this relationship replicated for Behavior and Desire, though the uniqueness regressions showed that past behavioral history, not current desire, is what is specifically linked to the Joyfulness factor. The cue utilizations (Figure 3) indicate that Fixation and Joyfulness were used by the raters to form their flirting rating for men, while only Joyfulness was used in the formation of this impression for women.

Taken together, the results from the Brunswikean lens model analyses imply that Fixation of a potential mate is a valid cue to male sociosexual Desire, which was used by our raters to infer flirtation. After controlling for the other two facets, a similar, but weaker and negative association existed in men for the explicit sociosexual Attitude. In women, Joyfulness during the conversation was a valid cue to past sociosexual Behavior that the

raters utilized when judging flirtation. The left half of Figure 3 summarizes the major relationships we found for men and women.

Sociosexuality effects on relationship status stability and change. To test whether sociosexuality predicts changes in romantic relationship status over one year, we compared the sociosexuality means between four groups: (1) those who were single at both t1 and t2 (*stable singles*, N = 78), (2) those who were in the same relationship at t1 and t2 (*in same relationship*, N = 114), (3) those who were in a new relationship at t2, no matter if they had been single or in a different relationship at t1 (*in new relationship*, N = 52), and those who were single at t2 because the relationship they had at t1 had ended (*single after separation*, N = 14). Two univariate ANOVAs with 4 (group) x 2 (sex) between-subject factors and either the SOI or the SOI-R total scores as dependent variables indicated that relationship status group had a significant effect in both cases (SOI: $F_{(3, 250)} = 12.56$, $p < .001$, $\eta_p^2 = .13$; SOI-R: $F_{(3, 250)} = 21.09$, $p < .001$, $\eta_p^2 = .20$), while the sex effect was significant for the SOI-R ($F_{(1, 250)} = 6.59$, $p = .011$, $\eta_p^2 = .03$), but not the SOI ($F_{(1, 250)} = 1.49$, $p = .22$) (cp. Table 2) and the group x sex interaction was not significant for either measure (Fs < 1). Bonferroni-adjusted pairwise comparisons of the means revealed that in both cases, those who were in the same relationship at t2 had lower global sociosexuality scores at t1 than those who remained single or who had found a new partner (ps < .001). In addition, those in a new relationship at t2 had marginally higher SOI total scores at t1 than those who were single after separation at t2 ($p = .054$; ps > .10 for all other pairwise comparisons).

Next, we ran a 4 (group) x 2 (sex) MANOVA with the three SOI-R facets as dependent variables. Relationship status group had a significant effect on Behavior ($F_{(3, 250)} = 13.82$, $p < .001$, $\eta_p^2 = .14$) and Desire ($F_{(3, 250)} = 35.91$, $p < .001$, $\eta_p^2 = .30$), but only a marginal effect on Attitude ($F_{(3, 250)} = 2.52$, $p = .058$, $\eta_p^2 = .03$). Sex effects were again significant for Attitude ($F_{(1, 250)} = 6.09$, $p = .014$, $\eta_p^2 = .02$) and Desire ($F_{(1, 250)} = 11.36$, $p < .001$, $\eta_p^2 = .04$), but not for Behavior ($F < 1$), while group x sex interactions were insignificant for all three facets (Fs < 1). Bonferroni-adjusted pairwise comparisons indicated that both those who had remained in the same relationship and those who had changed their relationship status from being in a relationship to single at t2 were lower on the Behavior facet at t1 than both those who had stayed singles or started a new relationship at t2 (all ps < .03). Furthermore, those in a stable relationship that prevailed until t2 were lower in their sociosexual Desire at t1 than the three other groups (all ps < .005). All other pairwise comparisons, including all for the Attitude facet, failed to reach significance (ps > .10). Effect sizes for the significant group differences were generally large (see Figure 4).

Figure 4 about here

Relationship status effects on sociosexuality stability and change. The 1-year rank-order stability for the SOI and the SOI-R was high in both men (SOI: $r = .74$, $p < .001$; SOI-R:

r = .83, p < .001) and women (SOI: r = .79, p < .001; SOI-R: r = .78, p < .001). On SOI-R facet level, rank-order stability was high for Behavior (men: r = .83, p < .001; women: r = .86, p < .001) and Attitude (men: r = .73, p < .001; women: r = .79, p < .001), but somewhat lower for Desire, especially in women (men: r = .68, p < .001; women: r = .39, p < .001). There was no significant mean level change in any total or facet score over the 1-year period for either men or women (all ts < 1.89, all ps > .06).

In order to test whether changes in romantic relationship status account for the imperfect rank-order stability of sociosexuality, we calculated change scores for the SOI, the SOI-R, and the three SOI-R facets by subtracting the t1 scores from the t2 scores, and compared mean levels in these change scores across the four relationship status groups (this data was available for N = 74 stable singles, N =110 in same relationship, N = 51 in new relationship, and N = 11 singles after separation). We first ran two 4 (group) x 2 (sex) ANOVAs, one with SOI total score change and one with SOI-R total score change as the dependent variables. In both analyses, relationship status group had a significant effect (SOI change: $F_{(3, 237)}$ = 8.14, p < .001, η_p^2 = .10; SOI-R change: $F_{(3, 237)}$ = 8.53, p < .001, η_p^2 = .10), while sex and the group x sex interaction had not (all Fs < 1.76, all ps > .10). Bonferroni-adjusted pairwise comparisons revealed that those who were singles after separation increased in their global sociosexuality compared to the other three groups (SOI: ps < .004, ds = .89-1.18; SOI-R: ps < .03, ds .94 to 1.46), while those in new relationships decreased in global sociosexuality more than the other three groups, though some of these latter comparisons were only marginally significant for the SOI (ps <.09, ds = .36-1.10; SOI-R: ps < .02, ds = .56-1.46; all other comparisons ps > .10).

We subsequently ran a 4 (group) x 2 (sex) MANOVA with change scores for the three SOI-R facets as dependent variables. Relationship status group had a significant main effect on changes in Behavior ($F_{(3, 237)}$ = 7.05, p < .001, η_p^2 = .08) and Desire ($F_{(3, 237)}$ = 15.80, p < .001, η_p^2 = .17), but not on Attitude change (F < 1). Sex had weak main ($F_{(1, 237)}$ = 7.25, p = .008, η_p^2 = .03) and interaction-with-group effects on Behavior change ($F_{(3, 237)}$ = 2.93, p = .03, η_p^2 = .04). There was also a marginally significant group x sex interaction on Desire change ($F_{(3, 237)}$ = 2.27, p = .081, η_p^2 = .03), while all other effects were not significant (ps > .10). Bonferroni-adjusted comparisons of the means indicated that men, but not women, who became single after separation increased in their Behavior scores between t1 and t2 compared to the other three groups (men: ps < .001, ds = 1.19-1.40; women: all ps > .10). Furthermore, those who had recently started a new relationship decreased in their sociosexual Desire compared to all other groups (ps < .001, ds = .96-1.84), while those who were single after separation showed a trend towards a stronger increase in their Desire compared to the stable singles (p = .09, d = .76) and those in stable relationships (p = .64, d = .83). Plots revealed that the effects on Desire change were somewhat more pronounced in

women than in men, which might explain the marginally significant interaction between group and sex. It should be noted again that the group of singles after separation was very small, so all effects involving this group should be interpreted with care.

Prediction of sexual behavior. Finally, we tested the predictive validity of the sociosexuality measures by examining the relation between their assessment at t1 and the number of sexual partners between t1 and t2. The criterion was measured by two items at t2: (1) SOI(-R) item 1 (asking for the total number of sexual partners in the past twelve months), and (2) an item asking for the number of new sexual partners in the past twelve months, with whom they never had intercourse before. Both items were log-transformed to reduced skew. They correlated .86 in men and .89 in women, and were thus aggregated after *z*-standardization within sex to form an index of *Future Sexual Partners*.

Future Sexual Partners was predicted by the total SOI (men: $r = .53$, $p < .001$; women: $r = .49$, $p < .001$) and SOI-R (men: $r = .57$, $p < .001$; women: $r = .39$, $p < .001$) scores at t1. The more differentiated perspective provided by the SOI-R facet-level correlations showed that the predictive validity was highest for the Behavior (men: $r = .58$, $p < .001$; women: $r = .45$, $p < .001$) and Desire (men: $r = .48$, $p < .001$; women: $r = .36$, $p < .001$) components, while it was lower for the Attitude component (men: $r = .27$, $p = .003$; women: $r = .17$, $p = .05$). The differences in effect sizes between Attitude and the other two facets were all significant (all *p*s < .03). To further corroborate these findings, we calculated uniqueness scores for all three facets by regressing each facet on the other two and saving the residuals (see Study 1). The uniqueness correlations revealed that Behavior (men: $r = .44$, $p < .001$; women: $r = .32$, $p < .001$) and Desire (men: $r = .32$, $p < .001$; women, $r = .24$, $p = .007$), but not Attitude (men: $r = -.02$, $p = .84$; women: $r = -.06$, $p = .52$), made a unique contribution to the prediction of Future Sexual Partners over the 1-year period.

Predictive validity of flirting behavior. If flirting is, as we argued, a more proximate behavioral criterion for sociosexuality, reflecting the active courtship patterns that initiate subsequent sexual contacts and new romantic relationships, our measure of flirting behavior should predict these outcomes. This link was indeed supported by our data: first, controlling for the dummy-coded confederate, the Global Flirting Rating predicted the reported Interest of the Confederate in the participant (men: $\beta = .30$, $p < .001$; women: $\beta = .44$, $p < .001$). This relationship remained significant for both sexes when facial attractiveness was simultaneously entered into the regression (see right half of Figure 3). Furthermore, the Global Flirting Rating at t1 predicted Future Sexual Partners (men: $\beta = .34$, $p < .001$; women: $\beta = .24$, $p < .001$), again independent of facial attractiveness (see right half of Figure 3).[4]

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[4] Global sociosexuality correlated significantly with facial attractiveness in men (SOI: $r = .19$, $p = .02$; SOI-R: $r = .19$, $p = .02$), but not in women (SOI: $r = -.15$, $p = .07$; SOI-R: $r = -.02$, $p = .86$). On facet

Finally, an ANOVA revealed that the Global Flirting Rating at t1 differed between relationship status groups at t2 ($F_{(3, 250)} = 12.57$, $p < .001$, $\eta_p^2 = .13$; sex had no main or interaction effects, *p*s > .10), with those who were single at both points or who found a new partner receiving a higher flirting rating in the lab than those who continued the same relationship or who stayed single after separation (*p*s < .05 for these Bonferroni-corrected pairwise comparisons). Since the amount of flirtation in our lab interaction was predictive of future mating outcomes, the predictive relationships between sociosexuality facets and flirting behavior can be regarded as consequential.

Partner effects. So far, we have analyzed the effects of global sociosexuality and its facets on mating success and relationship outcomes on the individual level. For those currently involved in a romantic relationship, this entails a simplification, since such dyadic relationships can be defined by the presence of effects that one partner has on the other (Kenny, Kashy & Cook, 2006).

One possible partner effect is that the mere involvement in a romantic relationship alters the effects that the individual level of sociosexuality has on behavior in the mating domain. Therefore, we reran all of the above analyses, controlling for romantic relationship status wherever appropriate. The general pattern of results remained unchanged.

Alternatively, it could be that not only one's own sociosexual orientation, but also the sociosexuality of his or her partner affects mating behavior and relationship outcomes. For example, having an unrestricted partner might motivate people to behave more unrestricted themselves or might increase their likelihood to terminate the relationship, independent of their own sociosexuality. Thus, we also analyzed potential effects of the partner's sociosexuality in the subsample of 70 couples. We applied Kenny et al.'s (2006) Actor-Partner Interaction Model (APIM) to test for such effects, using the SPSS 12.0 mixed procedure syntax they provided. In the APIM, effects that a characteristic of the target individual (actor) has on an outcome are disentangled from effects that a characteristic of his or her partner has on this outcome, and from interaction effects stemming from the specific combination of characteristics both partners bring into the relationship. We ran a series of APIMs, with either (1) the Global Flirting Rating, (2) relationship breakup during the next 12 months, or (3) the number of Future Sexual Partners as the dependent variable. We ran separate analyses for each SOI-R facet, yielding a total of nine analyses. In a first step, the actor's and partner's score on a SOI-R facet as well as their product were entered as predictors. In a second step, sex and its two- and three-way interactions with the other predictors were also entered. While several analyses indicated significant actor effects (which generally replicated the findings from the whole sample), partner effects and actor-

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level, only male Behavior showed a significant relationship to facial attractiveness ($r = 23$, $p = .007$). This pattern was even more obvious in the uniqueness correlations.

partner-interactions were significant in only three of the nine analyses. Detailed results for these three analyses, which also replicated when the uniqueness scores of the facet were used, are given in Table 6.

Table 6 about here

As can be seen in Table 6, the partner's sociosexual Attitude had a *negative* effect on the amount of flirtatious behavior the participants had displayed in the lab interaction, while there were no effects of the actor's Attitude, sex, or any interaction. This result could mean that those who are in a relationship with someone who expresses a very restrictive attitude are more likely to flirt with alternative mates, or (since both variable were concurrently assessed) that those who are more likely to flirt with strangers evoke a more restrictive attitude towards promiscuity in their partners. Different effects were found for sociosexual Desire: more unrestricted levels of Desire in either member of a couple increased the likelihood of a romantic breakup within the upcoming year. The significant interaction indicated that his effect was even more accentuated when both partners had unrestricted Desires, even though the weak three-way interaction suggests that the joint effect was somewhat stronger for men. Apparently, women are slightly more likely to terminate a relationship when only one partner has unrestricted desires. Similarly, both the actor's and the partner's Desire, as well as their interaction, predicted the number of sexual partners over the next 12 months. This might simply be a side-effect of lower relationship stability, or an indication that preferences for sexual (non-)exclusivity of one partner tend to have consequences for both.

Assortative mating. Given the existence of some partner effects, it is also interesting to have a look at the degree of assortative mating that exists for global sociosexuality and its facets. Assortative mating refers to the fact that mate choice for some characteristics is non-random, resulting in couples that resemble each other above chance level. Simpson and Gangestad (1991) reported a moderate degree of assortative mating for the SOI total score (r = .30). We failed to replicate this finding for the SOI (r = .13, p = .28), but found a similar degree of assortative mating for the SOI-R (r = .34, p = .004). An analysis on facet level revealed that only Attitude (r = .36, p = .002), but not Behavior (r = .10, p = .41) or Desire (r = .16, p = .18), showed significant within-dyad resemblances. This pattern of result was even more obvious in the correlations of the uniqueness scores (r = .01, .31, and .03 for Behavior, Attitude, and Desire, respectively). Thus, only the attitude component seems to be responsible for assortative mating on sociosexuality.

Discussion

Study 2 showed that Behavior, Attitude and Desire do not only emerge as components from the empirical structure of global sociosexuality measures and show distinct

correlational patterns with concurrently assessed self-reports, but are also predictive of mating behavior and romantic relationship outcomes in a highly differentiated manner. People with a history of unrestricted sociosexual behavior were more likely to stay single over the next year (when single) or to change partners (when in a relationship). Sociosexual desire was more restricted in those who will remain in their relationship for the next twelve months, while those who will separate tended to have desires almost as unrestricted as singles. Sociosexual attitudes, in contrast, did not predict future relationship status. Similarly, only past behaviors and current desires related to flirtatious behavior towards attractive strangers and future numbers of sex partners. After controlling for sociosexual behavior and desire, unrestricted attitudes had even a negative effect on flirting behavior. Within couples, a partner's restricted attitude apparently elicited (or was elicited by) flirtatious advances towards alternative mates. A partner with restricted sociosexual desire, on the other hand, facilitated a monogamous and stable romantic relationship. Finally, only the behavior and desire (which had the lowest temporal stability, especially in women) changed when the relationship status changed; attitudes remained the same. Assortative mating occurred only on attitudes. These results further confirm that the three components of global sociosexuality behave quite distinctively, indicating that they should be separated in the study of sociosexual orientations.

General Discussion

It might be a historical coincidence that sociosexuality has been treated almost exclusively as a broad, global construct. Kinsey introduced it as a descriptive dimension in his normative studies, and Simpson and Gangestad (1991) seemed to be inspired by a type approach when establishing the construct in psychology (see Gangestad & Simpson, 1990). In the following years, sociosexuality was more and more equated with mating strategies and tactics within an evolutionary life-history framework (Simpson et al., 2004). All these approaches enforce a global perspective on sociosexuality. On second sight, however, different aspects of sociosexuality do not need to be – and sometimes cannot be – closely interrelated. The most obvious contrast exist between sociosexual desire, which shows large sex differences in line with evolutionary expectations (Schmitt et al., 2003), and behavior, where every act of heterosexual sexuality requires a man and a woman. In every population with balanced sex ratio, the overall number of committed and uncommitted sexual acts will be the same for men and women, so it is impossible that every member of either sex behaves exactly as he or she desires (Asendorpf & Penke, 2005). Neither do explicit attitudes, which are likely more indicative of cultural and peer socialization, need to reflect desires or behaviors. Our studies provided strong support for a more differentiated perspective on sociosexuality. The three proposed sociosexuality components Behavior,

Attitude, and Desire were found in the empirical structure of the established SOI and also in the structure of our new SOI-R, which was able to assess them reliably. Furthermore, we showed that their contributions to the nomological network, the predictive validity, the longitudinal development, and the interpersonal effects of global sociosexuality are highly specific. In the following, we discuss the specifics separately for each sociosexuality facet:

Sociosexual Behavior. The Behavior facet, an index of the quantity of past short-term sexual encounters, shows strong and unique links to the diversity of past romantic and sexual relationships, as well as the occurrence of sexual infidelity. It can thus be regarded as a measure of the mating tactic an individual has implemented so far - or was able to implement. The trade-offs and difficulties that individuals face when trying to pursue their preferred mating tactic within competitive mating markets (Noë & Hammerstein, 1995; Penke et al., in press) are inferable from the facts that the correlation between sociosexual Desire and Behavior is rather low, and that the Behavior facet does not show the strong sex difference that is usually found for Desire. They are also reflected in the fact that traits that affect the initiation of mating interactions (like physical attractiveness, shyness, and sensation seeking) and self-perceptions of mate value relate to this facet (see also Gangestad & Simpson, 2000). Thus, the Behavior facet is as much an index of mating *potential* as it is of experiences.

Our results also showed that men and women who had more experience with short-term relationships in the past (i.e., those with high Behavior scores) were more likely to have multiple sexual partners and unstable relationships in the future. The behaviorally expressed level of sociosexuality thus seems to be a fairly stable personal characteristic. This stability seems to stem at least partly from the active behavior of individuals, since past sociosexual behavior also predicted the amount of flirtatious advances they showed towards an attractive stranger. For women, we could trace this relationship back to the amount of smiling and laughing they showed during an initial encounter. Smiling has been interpreted as a signal of low dominance and contact-readiness (Eibl-Eibesfeld, 1989), and it is perceived as attractive (O'Doherty et al., 2003). Furthermore, women tend to smile more when confronted with attractive men (Hazlett & Hoehn-Saric, 2000). One way to interpret these results it that women with more short-term mating experience might have learned how to use joyfulness to appear attractive and approachable for men they find attractive – successfully, as our confederates' ratings indicate - which in turn raises the odds for more unrestricted sociosexual behavior in the future.

Sociosexual Attitude. The unique contributions of the Attitude facet to the effects of sociosexual orientations were surprisingly limited. Some of the strongest correlations were found with other self-rated personality constructs. While it is reasonable that individuals adopt attitudes towards promiscuity that match their levels of sensation seeking, sex drive,

desire for sexual variety, shyness, and preference for exciting and attractive partners, it is striking that Attitude was the only sociosexuality facet which related to all kinds of self-report questionnaires. In sharp contrast, Attitude was the only sociosexuality facet that did not contribute uniquely to the prediction of future sexual behavior and relationship outcomes, and was even negatively related to flirting behavior when past behaviors and current desires were statistically controlled, indicating that people act against their explicit attitude when it contradicts their desires or behavioral histories. Furthermore, only the Attitude facet was unaffected by changes in the romantic relationship status, but men and women expressed a more restricted Attitude when their partners responded flirtatiously towards alternative mates or when conforming to religious values. Finally, sociosexual attitudes were solely responsible for the existence of assortative mating on sociosexuality. Whether this is a result of direct mate choice for partners that express a similar attitude, or an indirect effect of social homogamy (i.e., choosing a mate from within one's social environment – such as college, job, or neighbourhood – where others might share similar attitudes), remains unclear from the current data.

Taken together, this pattern of findings supports our argument that the unique aspect of sociosexual attitudes (which is not simply an explicit reflection of one's own behavior and desire) reflects social self-representation and cultural socialization – how people want to be seen by others, and how others have told them to be. This interpersonal-influence aspect of sociosexuality is important, since (1) the adaptive value of different sociosexual orientations differs between environments (Gangestad & Simpson, 2000; Schmitt, 2005a), which makes the cultural transmission of mating tactics valuable (Gangestad, Haselton & Buss, 2006), (2) men and women have to negotiate their conflicting desires when forming sexual relationships (Arnquist & Rowe, 2005; Buss & Schmitt, 1993), and (3) manipulating the sociosexual orientations of rivals can benefit one's own outcome within a competitive mating market (Baumeister & Twenge, 2002; Baumeister & Vohs, 2004). However, when it comes to what mating tactic someone will actually pursue, this component of sociosexuality apparently lacks predictive validity.

Sociosexual Desire. As expected, Desire showed the largest sex differences. It is likely that this facet drives the sex differences in global sociosexuality. Within sex, we could relate sociosexual Desire to general sex drive, desire for sexual variety, and sensation seeking. What was most compelling about this facet, however, were its transactions with romantic relationships: on the one hand, sociosexual Desire was more restricted in individuals who were currently in a relationship, became more restricted when a new relationship was started, and got more unrestricted again after about four years (consistent with Fisher, 1987) or when a break-up occurred. On the other hand, more unrestricted sociosexual Desires of both partners predicted relationship dissolution and sexual involvement with new partners.

Furthermore, Desire showed quite substantial negative correlations with concurrently assessed relationship quality, commitment, and fidelity, as well as weaker ones with attachment to the current partner.

Most of these personality-relationship-transactions were somewhat stronger in women than in men, which might explain the considerably lower temporal stability of Desire in women. This pattern of sex differences makes sense from an evolutionary perspective: focusing desire on a single long-term mate as long as the relationship is tenable aids basic female reproductive demands, like securing resources and paternal support (Buss & Schmitt, 1993; Trivers, 1972). For men, however, desiring short-term sexual encounters whenever they become attainable can yield high fitness payoffs. In support of this theoretical argument, male Desire was not only less reactive to romantic relationship status, it also predicted flirting behavior independent of their relationship status. The link between Desire and flirting was partly mediated by the amount of gazing towards a potential mate. Other studies have found that direct gaze, similar to smiling, indicates attraction, contact-readiness, and attention (Kleinke, 1986), and is perceived as attractive (Kampe, Frith, Dolan & Frith, 2001; Mason, Tatkow & Mccrae, 2005). However, contrary to smiling, direct gaze also signals dominance (Kleinke, 1986) - a trait women prefer in short-term mates (Gangestad, Garver-Apgar, Simpson & Cousins, 2007). This might explain why we found that sociosexuality predicts different flirtatious behaviors in men and women.

Implications and Limitations

The decomposition of global sociosexuality into three components has implications for future evolutionary psychological studies of individual differences in mating tactics. Differences in mating tactics reflect different solutions to life-history trade-offs, especially between investment in stable long-term relationships with high levels of parental investment versus less stable relationships with more or better partners. However, what is evolutionary relevant about mating tactics is only their behavioral implementation over the reproductive lifespan, since only actual behaviors affect reproductive success and ultimately fitness. Thus, sociosexual attitudes, desires, and also early (pre-reproductive) behavioral experiences can only affect fitness if they have an impact on actual reproductive behaviors. We provide the first evidence that sociosexual desire and past behavioral experiences indeed predict future mating behavior. Our study is also the first that shows that sociosexual orientations in general and sociosexual behavior in particular are fairly stable over a period as long as one year (shorter retest stabilities over six weeks and two months have already been reported by Ostovich & Sabini, 2004, and Simpson & Gangestad, 1991, respectively), and the first study that brings the developmental transactions between sociosexuality, romantic relationships, and flirting behavior into perspective. However, longitudinal studies over more extended time

periods are needed to shed light on how sociosexual orientations affect life-history decisions and trade-offs over the whole reproductive lifespan. This is especially important because most studies on sociosexuality have been conducted with about twenty year old undergraduate students (our participants had a more heterogeneous background, but those in Study 2 were only slightly older on average and all childless). At this age, mating behavior seldom leads to reproduction, but has a more exploratory character that is distinctive from the mating behavior with reproductive goals that occurs later in life (Arnett, 2000; Furman, 2002; Penke et al., in press). Indeed, Locke and Bogin (2006) argued that humans evolved an extended adolescent life phase to provide a “training period” for mating skills. Future studies should aim to understand how trade-offs in actual reproductive behaviors emerge from the interplay of sociosexual desires, attitudes, and past behavioral experiences.

The most central implication of our results is that studying sociosexuality as one unitary construct masks important effects that are specific to its components. It is also insufficient to separate only sociosexual behavior and attitude (as suggested by Webster & Bryan, in press, and Jackson & Kirkpatrick, 2007), since some of the most substantial effects were unique to sociosexual desire, while attitude itself lacked predictive validity for future behavior. This is especially critical since some studies rely exclusively on attitudinal items when assessing sociosexuality (e.g. Kurzban & Weeden, 2005; Rhodes, Simmons & Peters, 2005) or use sociosexuality measures that are heavily biased towards the attitude component (Bailey, Kirk, Zhu, Dunne & Martin, 2000).

While the three components of sociosexuality we propose may help to analyze mating tactics, they are ultimately not differentiated enough. Various motives can lead to similar levels of sociosexual behavior, attitude, and desire (Cooper, Shapiro & Powers, 1998; Greilling & Buss, 2000; Hill & Preston, 1996; Jones, 1998), and in the end they are the result of interacting systems of evolved psychological mating adaptations (e.g. Fisher, 2004; Gangestad, Thornhill & Garver-Apgar, 2005; Gangestad et al., 2007; Maner, Gailiot & DeWall, 2007; Penke et al., in press), genetic variance within these systems (Penke, Denissen & Miller, in press) and within general condition (Gangestad & Simpson, 2000), and social, cultural and ecological factors that evoke conditional responses (Gangestad & Simpson, 2000; Gangestad et al., 2006; Schmitt, 2005a). Our more differentiated perspective on sociosexuality provides one of the levels we need to explore in order to understand how evolution prepared the functional design of our species to exhibit complex adaptive mating behaviors.

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Appendix

The revised Sociosexual Orientation Inventory (SOI-R)

Please respond honestly to the following questions:

1. With how many different partners have you had sex within the past 12 months?
   - □ 0
   - □ 1
   - □ 2
   - □ 3
   - □ 4
   - □ 5-6
   - □ 7-9
   - □ 10-19
   - □ 20 or more

2. With how many different partners have you had sexual intercourse on *one and only one* occasion?
   - □ 0
   - □ 1
   - □ 2
   - □ 3
   - □ 4
   - □ 5-6
   - □ 7-9
   - □ 10-19
   - □ 20 or more

3. With how many different partners have you had sexual intercourse without having an interest in a long-term committed relationship with this person?
   - □ 0
   - □ 1
   - □ 2
   - □ 3
   - □ 4
   - □ 5-6
   - □ 7-9
   - □ 10-19
   - □ 20 or more

4. Sex without love is OK.
   □ 1 – Strongly disagree
   □ 2
   □ 3
   □ 4
   □ 5
   □ 6
   □ 7
   □ 8
   □ 9 – Strongly agree

5. I can imagine myself being comfortable and enjoying "casual" sex with different partners.
   □ 1 – Strongly disagree
   □ 2
   □ 3
   □ 4
   □ 5
   □ 6
   □ 7
   □ 8
   □ 9 – Strongly agree

6. I do *not* want to have sex with a person until I am sure that we will have a long-term, serious relationship.
   □ 1 – Strongly disagree
   □ 2
   □ 3
   □ 4
   □ 5
   □ 6
   □ 7
   □ 8
   □ 9 – Strongly agree

7. How often do you have fantasies about having sex with someone you are *not* in a committed romantic relationship with?
   □ 1 – never
   □ 2 – very seldom
   □ 3 – about once every two or three months
   □ 4 – about once a month
   □ 5 – about once every two weeks
   □ 6 – about once a week
   □ 7 – several times per week
   □ 8 – nearly every day
   □ 9 – at least once a day

8. How often do you experience sexual arousal when you are in contact with someone you are *not* in a committed romantic relationship with?
   □ 1 – never
   □ 2 – very seldom
   □ 3 – about once every two or three months
   □ 4 – about once a month
   □ 5 – about once every two weeks
   □ 6 – about once a week
   □ 7 – several times per week
   □ 8 – nearly every day
   □ 9 – at least once a day

9. In everyday life, how often do you have spontaneous fantasies about having sex with someone you have just met?
   □ 1 – never
   □ 2 – very seldom
   □ 3 – about once every two or three months
   □ 4 – about once a month
   □ 5 – about once every two weeks
   □ 6 – about once a week
   □ 7 – several times per week
   □ 8 – nearly every day
   □ 9 – at least once a day

Items 1-3 should be coded as 0 = 1, 1 = 2, ..., 10-19 = 8, 20 or more = 9; they can then be aggregated to form the Behavior facet. After reverse-coding item 6, items 4-6 can be aggregated to form the Attitude facet. Aggregating items 7-9 results in the Desire facet. Finally, all nine items can be aggregated as the total score of global sociosexual orientation.

When items 1-3 are presented with open response format instead of the rating scales, items 2, 4, and 7 of the original SOI (Table 1) can be added to the SOI-R to allow for calculating the SOI total score in addition to the SOI-R scores. In this case, the open responses should be recoded to the rating scale format (i.e., 0 = 1, 1 = 2, ..., 20 to max = 9) before the SOI-R scores are determined.

Alternatively, we also developed a version of the SOI-R with 5-point rating scales, which might be more appropriate for samples with less educated or less test-experienced subjects. In this version, the scale alternatives are “0”, “1”, “2-3”, “4-7”, and “8 or more” for the Behavior items, 1 (strongly disagree) to 5 (strongly agree) for the Attitude items, and “never”, “very seldom”, “about once a month”, “about once a week”, and “nearly every day” for the Desire item. In a large, heterogeneous online sample (*N* = 8,549), the SOI-R with five response alternatives per item achieved good internal consistencies (α = .83, .81, .82, and .85 for the total score and the facets Behavior, Attitude, and Desire, respectively).

Author Notes

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Table 1: The Sociosexual Orientation Inventory (SOI).

Item	Text
1	With how many different partners have you had sex (sexual intercourse) within the past year? [a]
2	How many different partners do you foresee yourself having sex with during the next five years (Please give a *specific, realistic* estimate)? [a, b]
3	With how many partners have you had sex on *one and only one* occasion? [a]
4	How often do you fantasize about having sex with someone other than your current dating partner? [c]
5	Sex without love is OK. [d]
6	I can imagine myself being comfortable and enjoying "casual" sex with different partners. [d]
7	I would have to be closely attached to someone (both emotionally and psychologically) before I could feel comfortable and fully enjoy having sex with him or her. [d, e]

Notes: [a]: open response format, [b]: usually trimmed at 30, [c]: Rating scale from 1 (never) to 8 (at least once a day), [d]: rating scale from 1 (I strongly disagree) to 9 (I strongly agree), [e]: reverse coded.

Table 2: Descriptive statistics and sex differences of the sociosexuality measures in both studies.

	No.	Men			Women			Sex difference	
	items	α	*M*	*SD*	α	*M*	*SD*	*t*	Cohen's *d*
Study 1									
SOI-R Behavior	3	.85	2.76	1.83	.84	2.65	1.73	1.62	.06
SOI-R Attitude	3	.87	6.42	2.33	.83	5.41	2.37	1.81***	.43
SOI-R Desire	3	.86	5.62	1.91	.85	3.96	1.94	21.72***	.86
SOI-R total score	9	.83	4.93	1.50	.83	4.01	1.52	15.49***	.61
SOI	7	.76	57.03	49.78	.75	45.23	39.10	6.46***	.27
Study 2									
SOI-R Behavior	3	.85	3.09	1.88	.79	3.10	1.64	.04	.00
SOI-R Attitude	3	.76	6.99	1.79	.88	6.26	2.36	2.92**	.35
SOI-R Desire	3	.86	4.98	1.88	.83	3.97	1.82	4.61***	.55
SOI-R total score	9	.83	5.02	1.40	.84	4.44	1.49	3.36***	.40
SOI	7	.75	59.23	40.56	.76	51.37	40.32	1.63	.19

Notes: **: $p < .01$, ***: $p < .001$.

Table 3a: Correlates of sociosexuality and its components for the men in Study 1

	Zero-order correlations					Uniqueness correlations		
	SOI	SOI-R	SOI-R B	SOI-R A	SOI-R D	SOI-R B	SOI-R A	SOI-R D
No. prior romantic relationships	.39***	.35***	.46***	.25***	.07	.40***	.08	-.03
No. prior sexual partners	.68***	.59***	.86***	.38***	.09**	.77***	.07	-.07
No. prior extra-pair sexual partners	.53***	.43***	.61***	.26***	.12***	.55***	.02	.01
Self-Perceived Mate Value Scale	.24***	.23***	.34***	.16***	.03	.27***	.07	-.01
Religiosity	-.07	-.17***	-.07	-.21***	-.08	.01	-.19***	.00
Attachment preference factor [a]	-.03	-.08	-.02	-.10	-.05	.01	-.09	-.01
Resources preference factor [a]	.09	-.01	.09	-.08	.00	.11	-.11	.03
Condition preference factor [a]	.02	.19***	.08	.21***	.10	.02	.17**	.01
Short-Term Mating Index [b]	.33***	.70***	.34***	.67***	.52***	.06	.45***	.30***
Sensation Seeking Scale [b]	.32***	.53***	.35***	.49***	.32***	.15***	.31***	.15***
Shyness Scale [b]	-.25***	-.27***	-.30***	-.23***	-.07	-.22***	-.12**	.02
Sex Drive Questionnaire [b]	.22***	.42***	.15***	.32***	.46***	.01	.15***	.37***
Masturbation frequency	.07	.22***	-.01	.13***	.38***	-.07	.01	.36***
Only men in a romantic relationship								
Personal Relationship Quality Components	-.06	-.23***	-.03	-.16***	-.32***	.04	-.05	-.29***
Current partner is “Mrs. Right”	-.12**	-.23***	-.05	-.20***	-.26***	.03	-.11	-.21***
could imagine to be unfaithful	.26***	.54***	.29***	.45***	.48***	.12	.23***	.36***
been unfaithful in this relationship	.24***	.32***	.35***	.18***	.23***	.30***	-.02	.18***
Sexual intercourse frequency	.10	.12**	.16***	.16***	-.03	.10	.14**	-.10
Secure attachment style (RQ)	.07	-.03	.05	-.02	-.08	.06	-.02	-.09
Fearful attachment style (RQ)	.06	.16***	.08	.09	.21***	.04	-.01	.20***
Preoccupied attachment style (RQ)	-.04	.00	-.03	-.06	.08	.00	-.09	.11
Dismissive attachment style (RQ)	.04	.17***	.04	.18***	.15***	-.03	.12**	.11
RQ - Model of self	.03	-.01	.01	.05	-.09	.00	.09	-.12***
RQ - Model of other	-.04	-.18***	-.05	-.17***	-.17***	.02	-.11	-.13***

Notes: N = 1,026; men in a romantic relationship: N = 528; [a]: N = 316; [b]: N = 709.

B: Behavior facet, A: Attitude facet, D: Desire facet, RQ: Relationship Questionnaire

**: $p < .01$, ***: $p < .001$. p-levels ≥ .01 are not reported.

Table 3b: Correlates of sociosexuality and its components for the women in Study 1

	Zero-order correlations					Uniqueness correlations		
	SOI	SOI-R	SOI-R B	SOI-R A	SOI-R D	SOI-R B	SOI-R A	SOI-R D
No. prior romantic relationships	.26***	.23***	.38***	.20***	-.05	.33***	.05	-.13***
No. prior sexual partners	.62***	.56***	.83***	.42***	.05	.72***	.04	-.10***
No. prior extra-pair sexual partners	.49***	.41***	.57***	.31***	.07	.48***	.04	-.04
Self-Perceived Mate Value Scale	.16***	.19***	.23***	.15***	.06	.15***	.03	.04
Religiosity	-.15***	-.18***	-.16***	-.18***	-.05	-.08	-.12***	.01
Attachment preference factor [a]	-.15***	-.23***	-.16***	-.23***	-.13**	-.05	-.15***	-.05
Resources preference factor [a]	.01	-.05	.01	-.07	-.03	.06	-.09	.00
Condition preference factor [a]	.16***	.25***	.11**	.23***	.20***	.00	.15***	.13**
Short-Term Mating Index [b]	.41***	.68***	.30***	.65***	.52***	-.03	.46***	.33***
Sensation Seeking Scale [b]	.31***	.46***	.31***	.43***	.28***	.11***	.27***	.14***
Shyness Scale [b]	-.15***	-.21***	-.21***	-.19***	-.08	-.14***	-.09**	-.01
Sex Drive Questionnaire [b]	.26***	.33***	.22***	.24***	.29***	.11***	.09**	.22***
Masturbation frequency	.18***	.24***	.11***	.14***	.30***	.04	.01	.28***
Only women in a romantic relationship								
Personal Relationship Quality Components	-.21***	-.28***	-.14***	-.13***	-.40***	-.08	.03	-.37***
Current partner is “Mr. Right”	-.21***	-.27***	-.11**	-.16***	-.36***	-.02	-.03	-.32***
could imagine to be unfaithful	.32***	.45***	.21***	.32***	.51***	.04	.14***	.41***
been unfaithful in this relationship	.31***	.39***	.30***	.24***	.37***	.19***	.04	.30***
Sexual intercourse frequency	.09**	.05	.12***	.07	-.07	.09**	.05	-.10**
Secure attachment style (RQ)	-.08	-.08	-.03	-.05	-.10**	.00	-.02	-.09**
Fearful attachment style (RQ)	.11**	.11***	.07	.06	.13***	.04	-.01	.12***
Preoccupied attachment style (RQ)	.06	.04	.03	.00	.08	.03	-.03	.08
Dismissive attachment style (RQ)	.19***	.27***	.16***	.22***	.24***	.05	.12***	.17***
RQ - Model of self	-.02	.02	.01	.05	-.02	-.02	.06	-.05
RQ - Model of other	-.16***	-.21***	-.11***	-.16***	-.20***	-.03	-.08	-.15***

Notes: N = 1,682; women in a romantic relationship: N = 919; [a]: N = 551; [b]: N = 1,131.

B: Behavior facet, A: Attitude facet, D: Desire facet, RQ: Relationship Questionnaire.

**: $p < .01$, ***: $p < .001$. p-levels ≥ .01 are not reported.

Table 4: Accuracies and cue validities for all Brunswickean lens model analyses in Study 2.

	Betas for scales scores					Betas for uniquenesses		
	SOI	SOI-R	SOI-R B	SOI-R A	SOI-R D	SOI-R B	SOI-R A	SOI-R D
Men								
Global Flirting Rating	.27**	.33***	.28**	.06	.41***	.20*	-.18*	.38***
Behavior coding: Fixation	.09	.14	.05	-.04	.28***	.01	-.18*	.33***
Behavior coding: Expressivity	.10	.10	.07	-.02	.16†	.05	-.11	.18*
Behavior coding: Joyfulness	-.02	.06	-.05	.07	.11	-.09	.04	.10
Behavior coding: Inhibitedness	.01	.02	-.04	.05	.03	-.07	.05	.03
Women								
Global Flirting Rating	.26**	.17*	.28***	.02	.14†	.28***	-.14†	.07
Behavior coding: Fixation	.10	.11	.12	.16	-.01	.06	.13	-.08
Behavior coding: Expressivity	-.04	-.14	-.11	-.10	-.13	-.05	-.04	-.09
Behavior coding: Joyfulness	.27**	.17*	.26**	.02	.21*	.24**	-.14	.15
Behavior coding: Inhibitedness'	-.07	-.05	-.08	.01	-.04	-.09	.05	-.02
Behavior coding: Flirting gestures	.08	-.02	.06	-.03	-.02	.09	-.06	-.03

Notes: All beta weights are controlled for the confederate during the conversation (dummy-coded).

†: $p < .10$, *: $p < .05$, **: $p < .01$, ***: $p < .001$.

Table 5: Descriptive statistics and factor structure of the behavioral codings in Study 2.

	Men							Women							
	M	*SD*	Factor 1 Fixation	Factor 2 Express-ivity	Factor 3 Joyfulness	Factor 4 Inhibited-ness	λ	*M*	*SD*	Factor 1 Fixation	Factor 2 Express-ivity	Factor 3 Joyfulness	Factor 4 Inhibited-ness'	Factor 5 Flirting gestures	λ
Proportion of time:															
Facial gazing	.69	.18	**.90**	-.09	-.07	-.05	.82	.75	.16	**.90**	-.08	.01	-.01	-.03	.81
Speaking	.50	.13	-.22	**.76**	.31	-.06	.72	.51	.13	-.23	**.82**	.07	-.18	-.09	.77
Silence	.09	.06	-.47	**-.54**	.10	-.18	.56	.14	.10	-.26	**-.70**	.01	-.06	.04	.56
Smiling	.17	.13	.34	-.28	**.68**	.09	.67	.19	.13	.12	-.32	**.74**	-.08	-.04	.66
Laughing	.01	.02	.04	-.07	**.61**	-.08	.39	.02	.03	-.01	.17	**.77**	-.08	-.03	.62
Illustrators	.05	.06	.07	**.64**	-.06	.02	.41	.06	.07	-.09	**.69**	-.07	-.09	-.11	.51
Body adaptors	.07	.14	-.15	-.10	-.08	**.76**	.61	.08	.13	-.16	-.12	-.02	**.74**	.02	.59
Object adaptors	.01	.09	.13	.26	.07	-.10	.10	.04	.15	.00	-.03	-.36	-.21	-.18	.21
Facial adaptors	.02	.04	-.12	.41	-.09	.10	.20	.03	.05	.00	.42	.04	.14	.21	.25
Frequency:															
Short glances	5.32	5.36	**-.87**	.01	.04	.02	.76	4.44	4.44	**-.85**	-.04	-.08	.04	.03	.74
Look through	.02	.15	-.08	.00	-.01	-.29	.09	.01	.08	.07	-.04	-.08	**.62**	.10	.41
Interactive gestures	.24	.56	-.19	.31	.04	-.16	.16	.20	.48	.04	.12	.10	**.66**	-.20	.51
Hair flip/toss	.03	.34	-.07	.07	.19	-.02	.05	.18	.70	.14	.05	.09	-.09	**.79**	.66
Coy smile	.16	.60	-.06	.06	.05	**.76**	.58	.22	.86	-.19	-.12	-.05	.03	**.71**	.56
Backchanneling	9.88	6.25	.34	-.27	**-.69**	-.17	.70	1.38	6.08	.43	-.44	-.43	.09	.08	.58
% variance explained			14.54	11.96	9.96	9.08				12.98	14.60	9.94	10.07	8.57	

Notes: Factor loadings ≥ .50 are printed in bold face.

Table 6: Hierarchical modeling of actor, partner, sex and interaction effects of sociosexuality facets on outcome variables in Study 2

	Model 1		Model 2	
	b	*SE*	*b*	*SE*
Flirting behavior rating				
Intercept	-.355	.086	-.337	.089
Actor SOI-R Attitude	-.009	.035	-.004	.035
Partner SOI-R Attitude	-.080*	.033	-.084*	.037
Actor X Partner	.006	.015	.004	.015
Sex			-.097	.072
Actor X Sex			.008	.038
Partner X Sex			-.002	.039
Actor X Partner X Sex			.008	.012
Relationship breakup				
Intercept	.135***	.037	.139***	.041
Actor SOI-R Desire	.061***	.016	.062***	.017
Partner SOI-R Desire	.048**	.016	.046**	.017
Actor X Partner	.030*	.013	.031*	.013
Sex			-.008	.011
Actor X Sex			-.014	.018
Partner X Sex			-.004	.018
Actor X Partner X Sex			.008*	.004
Number of future sex partners				
Intercept	-.416***	.070	-.403***	.079
Actor SOI-R Desire	.142***	.037	.136***	.039
Partner SOI-R Desire	.107**	.038	.112**	.041
Actor X Partner	.065*	.026	.065*	.026
Sex			.028	.057
Actor X Sex			-.010	.041
Partner X Sex			.018	.042
Actor X Partner X Sex			.015	.019

Notes: Breakup is dummy coded (0 = no breakup, 1 = breakup). Sex is dummy coded (1 = male, -1 = female). All predictors are centered on dyad level. Only models with significant partner effects are shown.

*: $p < .05$, **: $p < .01$, ***: $p < .001$.

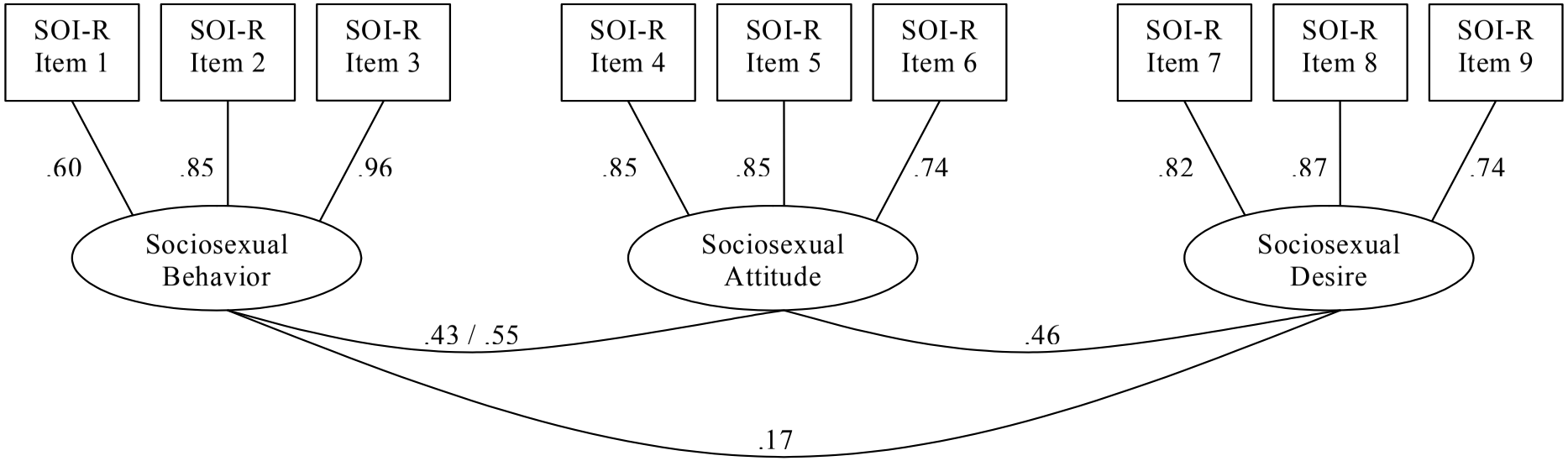

Figure 1: Confirmatory Factor Analysis of the Revised Sociosexual Orientation Inventory (SOI-R).

Notes: All factor loadings and correlations are significant at p < .001. The two correlations between the sociosexual behavior and attitude factors are for men and women, respectively. The difference is significant at < .001.

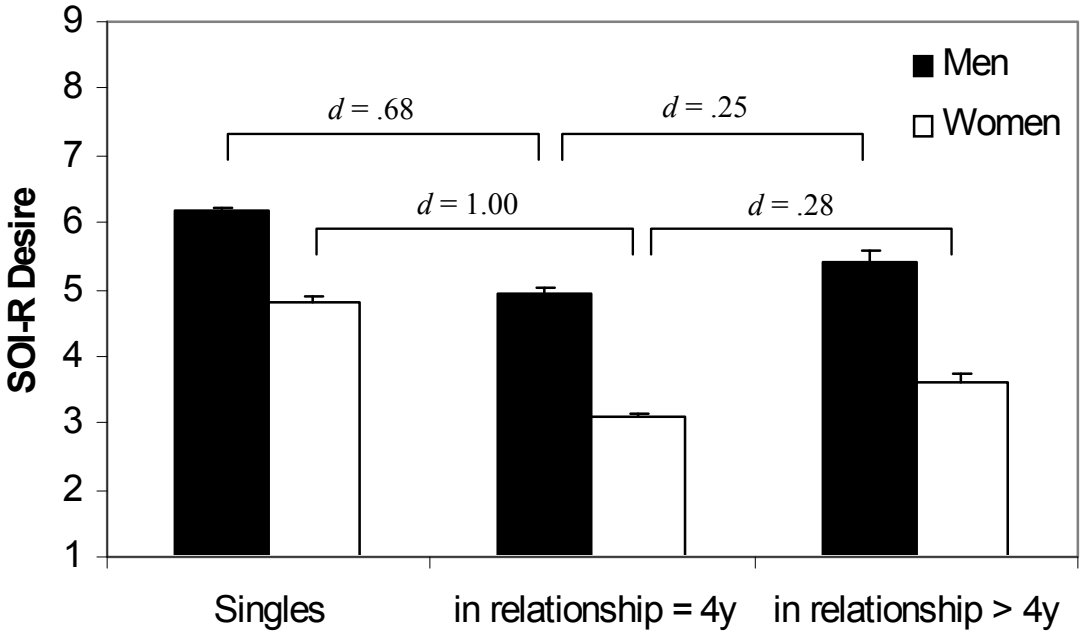

Figure 2: Effects of relationship status and duration on sociosexual desire in Study 1.
Notes: All sex and group differences p < .001.

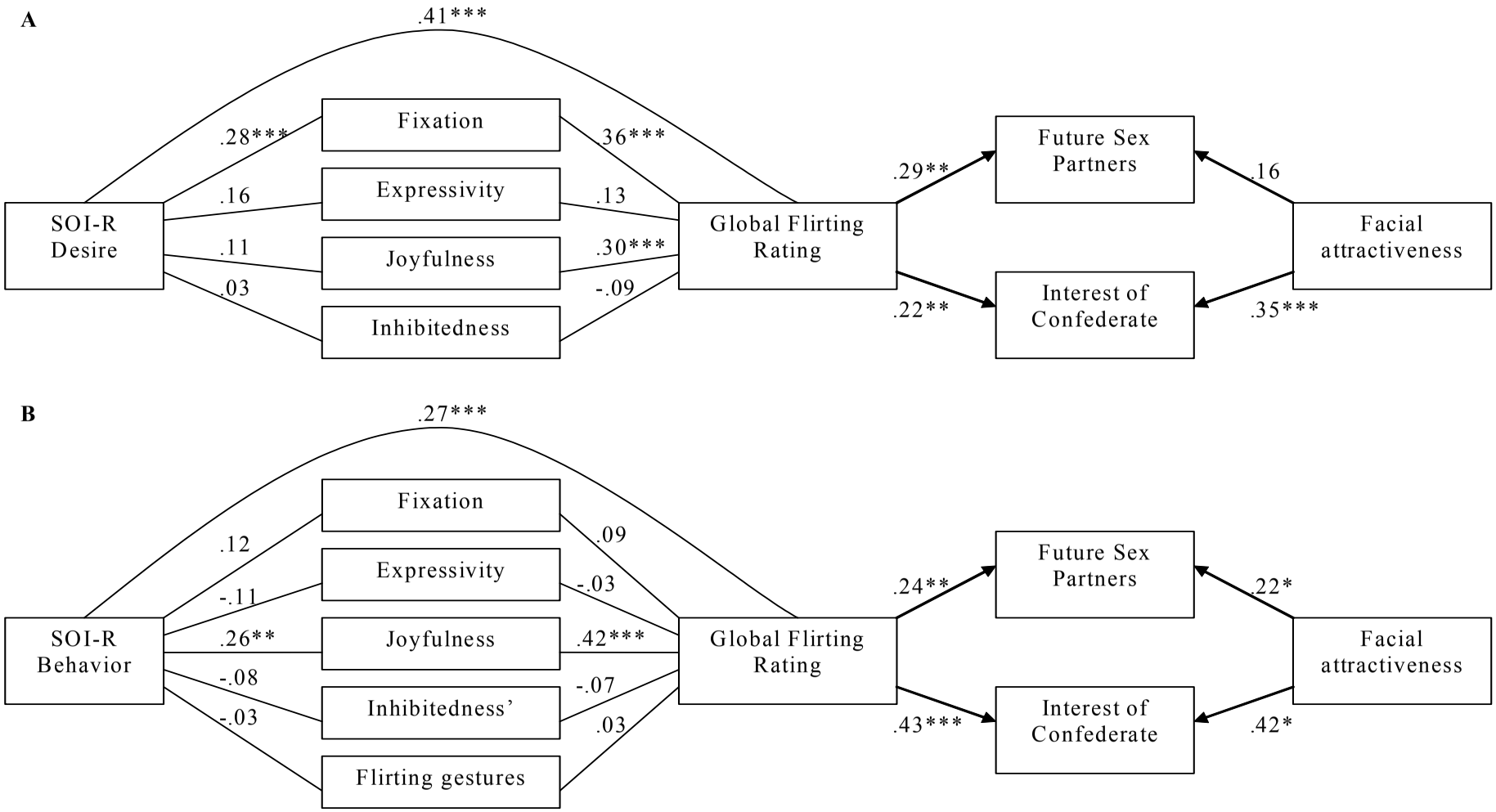

Figure 3: Significant links between sociosexuality, flirting behavior, and mating success in Study 2.

Notes: Panel A: men. Panel B: women. *: *p* < .05, **: *p* < .01, *: *p* < .001.**

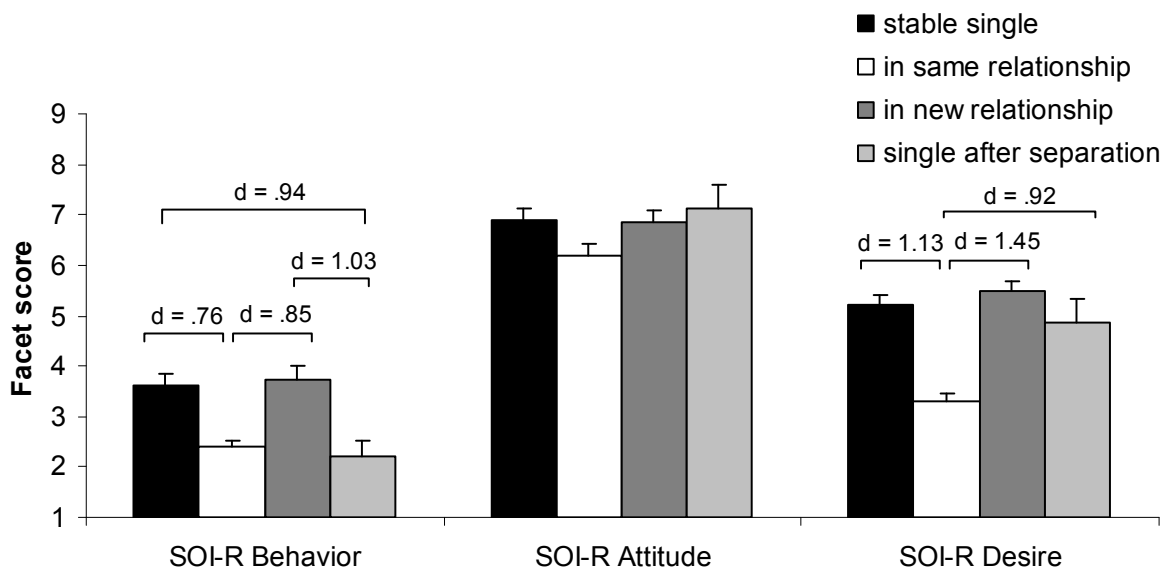

Figure 3: Mean differences in the SOI-R facets between relationship status groups in Study 2. Notes. Groups refer to the relationship status 12 months after the assessment of the SOI-R. Effect sizes (Cohen's *d*) are given for all significant ($p < .05$) group differences.