Mental traits as fitness indicators: Expanding evolutionary psychology's adaptationism
By Geoffrey Miller

Abstract

According to most evolutionary psychologists, human psychological adaptations can be recognized by criteria such as high efficiency, high complexity, high modularity, low phenotypic variance, low genotypic variance, low heritability, universality across cultures, and universality across individuals. These criteria are appropriate for adaptations that have been shaped through stabilizing selection for survival utility. However, they are often inappropriate for adaptations that have been shaped by sexual selection through mate choice as reliable signals of heritable fitness. If some psychological adaptations evolved as sexually-selected fitness indicators of this type, we should expect them to violate many standard criteria used by evolutionary psychology to distinguish adaptations from non-adaptations. This paper addresses the problems raised by new developments in sexual selection theory and animal signaling theory for evolutionary psychology's adaptationism. It suggests our adaptationist criteria must recognize two typical kinds of psychological adaptations: naturally selected survival mechanisms and sexually selected fitness indicators.

Introduction: The standard adaptationist criteria

Adaptation has been the key concept in evolutionary theory ever since Darwin (Williams, 1966). Evolutionary psychology has rightly stressed that the "psychological adaptation" should be the key concept in any science of human nature (Cosmides & Tooby, 1994; Tooby & Cosmides, 1990a, 1990b, 1992). Yet evolutionary psychology also recognizes that not all human behavior is the direct outcome of an evolved psychological adaptation. Many behaviors are individually acquired. Others are pathological results of genetic mutation or neurological damage. The central methodological challenge in evolutionary psychology has been the identification of criteria that distinguish psychological adaptations from non-adaptations.

The stakes are high in this game of criterion-setting. If a human mental trait is accepted as a legitimate psychological adaptation, it can be admitted into the pantheon of human nature. Its biological legitimacy renders it worthy of intense study. It becomes a defining feature of the human condition. On the other hand, if a class of human behavior is not accepted as the product of a legitimate adaptation, it may be marginalized to the netherworld of the merely individual or the merely cultural. Assuming psychology is striving to be a nomothetic science that seeks lawful knowledge about human nature, and that seeks consilience with the rest of biology, the limits of adaptationism set, to a first approximation, the limits of psychology itself. Behaviors that do not emerge from psychological adaptations tend to be culturally local, historically transitory, or pathological – the stuff of cultural criticism, market research, or psychiatry.

This raises problems for certain human behaviors and psychological phenomena that are culturally, socially, sexually, economically, and emotionally important, but that do

not fit the current standard criteria for psychological adaptations. These marginalized behavioral phenomena include things like art, music, humor, sports, religion, intelligence, creativity, and kindness. Basically, the problem is that some people are very much better at these things than others. Yet if they were legitimate psychological adaptations, standard evolutionary psychology predicts a uniformity of functional design that would forbid such extravagant variation (Miller, 1997, 1998a, in press).

Many of our most cherished human abilities do not seem to qualify as adaptations according to the adaptationist criteria that have become standard in evolutionary psychology (e.g. Buss, 1995; Pinker, 1997; Thornhill, 1997; Tooby & Cosmides, 1990a, 1990b, 1992). These criteria usually include the following: (1) high efficiency, (2) high complexity, (3) high modularity, (4) low phenotypic variance, (5) low genotypic variance, (6) low heritability, (7) universality across cultures, (8) universality across pre-history and history, (9) universal, spontaneous development in all normal environments according to standardized developmental stages, (10) a functional design that would, on average, have promoted survival or reproductive success under ancestral conditions. As with psychiatric disorders, an adaptation need not fit all ten major diagnostic criteria, but it is expected to fit most of them. These adaptationist criteria have evolutionary rationales largely derived from natural selection theory rather than sexual selection theory or signaling theory. To assess these criteria, I will first review the basic concept of a sexually selected fitness indicator, and then see whether the traditional criteria are applicable to such indicators.

Indicators as adaptations

Over the past few years, biologists studying sexual selection and animal signaling systems have recognized a new class of adaptations called indicators (Andersson, 1994; Grafen, 1990; Hauser, 1997; Johnstone, 1995; Zahavi & Zahavi, 1997). These often look rather different from standard naturally selected mechanisms that solve standard survival problems. The evolved function of indicators is basically to advertise an individual's fitness to other individuals. Usually, the incentives for doing this are to deter a predator from pursuing one, to intimidate a sexual rival, or to attract a sexual mate.

In all three cases, strategic issues arise concerning the reliability of fitness indicators. Every individual would simulate high fitness if it could. Such simulation would deter predators from pursuing it, by making it appear difficult to catch. Similarly, apparent high fitness would discourage sexual rivals and attract sexual partnerrs. This is because mate preferences generally evolve to favor fitness indicators that could result in one's offspring inheriting better than average genes, which would be manifest in higher than average fitness. However, if all animals could produce an appearance of high fitness by using a particular indicator, there would no longer be any reason for other animals to pay any attention to that indicator (Zahavi & Zahavi, 1997; Miller, 1998a). The indicator would no longer convey reliable fitness information, so would offer no good basis for mate choice. Thus, over the long run, indicators must be reliable in order to be effective as signals.

There are basically just two ways to make fitness indicators reliable. They can be either strategic handicaps or revealing handicaps (Johnstone, 1995). A strategic handicap is an indicator that has a higher relative costs for a low-fitness individual than it does for a high-fitness individual. For example, luxury goods in modern consumerist societies function as strategic handicaps that reliably indicate the wealth of their owners (Veblen, 1899). A poor individual cannot afford a Ferrari, whereas a rich individual can, so legitimate ownership of a Ferrari reliably indicates wealth. The strategic handicap idea depends on the notion that fitness is relatively fungible like money so it can be re-

allocated from one trait to another. This re-allocation could happen during the life of the individual (by directing nutrients and energy from one trait to another), or over evolutionary time, through heritable modifications in a body's growth and maintenance priorities.

Revealing handicaps are rather different. They cannot be faked because of some fundamental biological correlation between a component of fitness and an element of the signal. For example, the ability to win a gold medal in the Olympic decathlon is a reliable indicator of physical fitness. At the moment, there is no way that a human with high mental ability but moderate physical ability (such as Bill Gates) could transfer some excess mental energy or excess money into physical energy to win such a contest. Nor could they simply buy a gold medal and pretend to have won, because too many spectators watch the Olympics. Revealing handicaps are reliable because fitness is not completely fungible within a lifetime, and because some biological constraints are resistant to change over evolutionary time. Biologists debate whether specific displays like orange-red caretenoid colors are strategic handicaps, revealing handicaps, or neither (e.g. Olson & Owens, 1998), but few challenge the importance of reliability in sexual signaling.

Perceptual issues also arise concerning the discriminability of fitness indicators. A signal is useless if receivers of the signal cannot discriminate between the signal and its absence (Hauser, 1997). Generally, the most useful signals for deterring predators, intimidating rivals, and attracting mates will be those that can be perceived at a distance through visual, auditory, or olfactory channels. The most useful signals for advertising fitness, which is a continuous variable, may often have continuously variable elements that can be easily discriminated, such as color intensity, sound loudness, or pheromone concentration. Thus, indicators must vary within a population in order to convey fitness information.   The variation must not be subtle but obvious. It must be perceivable at a distance. It must be variation by design, not by accident. Indicators are adaptations that evolved precisely in order to display maximum perceivable variation within a population.

Adaptationism from a sexual signaling viewpoint

Given the elements of sexual selection theory and animal signaling theory, we are now in a position to critically assess the standard adaptationist criteria proposed by evolutionary psychology for identifying psychological adaptations. My strategy will be to ask which of these criteria would succeed in identifying a sexually selected fitness indicator as a legitimate biological adaptation. If a criterion is systematically biased to exclude such indicators, then we have a methodological problem on our hands.

The engineering criteria

The engineering criteria (efficiency, complexity, and modularity) derive from Darwin's desire to explain the appearance of complex organic design through a natural selection process that requires no designer. Yet the assessment of these engineering criteria depends on two difficult steps: (1) postulating some adaptive problem that the adaptation has evolved to solve, and (2) assessing the likelihood that the adaptive problem could have been solved "by chance", without specific selection pressures having shaped the adaptation. If the adaptive problem is misidentified, the wrong assessment may be given about whether a trait is an adaptation. For morphological traits, it may be reasonably easy to discern whether a trait is too complex, too efficient, or too well designed to be due to "chance".   But for psychological capacities, it is often difficult to determine whether the capacity is too well-designed to be a "chance" side-effect of other adaptations, such as adaptations for skill learning.

The criteria of efficiency, complexity, and modularity probably still apply to sexually-selected fitness indicators, but nobody knows yet quite how. The proper use of these criteria depends on seeing sexually-selected indicators as adaptations for courtship and mating, and not as side-effects of survival adaptations. In the past, Herbert Spencer's memorable but misleading phrase "survival of the fittest" led many researchers to seek survival functions for psychological adaptations. When no plausible survival function can be found, the trait may often be dismissed as a non-adaptation. For over a century, this led to almost every sexually-selected trait being dismissed as non-adaptive (Cronin, 1991).

Efficiency

Only recently have biologists started to understand animal signaling well enough to imagine ways of assessing the efficiency of fitness indicators (Hauser, 1997; Johnstone, 1995). A major point of confusion is the requirement that strategic handicaps must be costly in order to be reliable. From the signaling point of view, the high fitness costs of strategic handicaps are what make them efficient as fitness indicators. But from a traditional adaptationist viewpoint, these high fitness costs look inefficient. The potential for confusion is clear if we take an example of conspicuous consumption like Ferrari-ownership. If one asks whether a Ferrari is an efficient mode of transportation, the answer is surely not: it is very poor value for money, imposes high insurance and maintenance charges, and gets poor gas mileage. But if we ask whether a Ferrari is an efficient indicator of wealth, the answer is certainly yes. It is very easy to buy one if you can afford it (Ferrari dealerships are reasonably common and very friendly to the rich), but impossible if you cannot. Even if a poor man steals a Ferrari, he could not afford the maintenance, insurance, and gas costs for very long. The Ferrari is also efficient from the signal-assessor's point of view: it is visible from a distance, easily discriminable from other cars, and commonly understood to be expensive. The assessment of an adaptation's efficiency depends critically on knowing what the adaptation's function is. This is doubly true for fitness indicators, which look ridiculously wasteful and inefficient in every domain other than fitness-signaling.

Complexity

The complexity criterion also applies to fitness indicators in a rather different way than it applies to ordinary adaptations. Basically, ordinary adaptations evolve complexity because it is a complicated matter to achieve a significant fitness-enhancing effect in a complex world. For example, predators evolve complex bodily and behavioral adaptations for catching prey because prey avoid being caught and their reluctance must be overcome by orchestrating a complex series of worldly events including tracking, identification, pursuit, capture, dismemberment, swallowing, and digesting. To a large extent, ordinary adaptations have to be complex because the world offers little help in solving an animal's adaptive problems.

The complexity that selection demands of fitness indicators has a rather different texture. Indicators promote an animal's fitness by influencing mate choice mechanisms in opposite-sex conspecifics. Their effects are psychological, not physical. This means that sometimes, the complexity of a signal system can be spread between the behavioral adaptations of the signaler and the perceptual psychology of the receiver (Hauser, 1997).   For example, receivers often have an interest in perceiving signals such as fitness indicators. Females evolved to perceive and judge male courtship displays, because the fitness of their offspring depended on them finding a high-quality mate. Sometimes, very simple (but costly) signals can succeed because receivers have evolved to internalize a lot of tacit knowledge about the signalling system, particularly the

fitness information conveyed by signals. A diamond engagement ring is not a particularly complex artifact, but as a sexual signal, it conveys a rich set of information about its sender and his intentions to its receiver, because the receiver already knows a lot about the cost of diamonds and the conventions of marriage. By pushing the complexity of the signal system into the heads of sympathetic receivers, the signal itself could be quite simple. If we then assessed this engagement-ring signal narrowly, according to traditional complexity criteria, we might be rather unimpressed. However, if we view the signal in context as part of a system that resides mostly in the heads of receivers and signallers, we may be more generous in accepting it as a well-designed adaptation.

For fitness indicators that aim to create an impression of how an animal ranks along a single quantitative variable, there is not really much information to convey, so the signal itself need not be very complex. Nor need the signal-production equipment be very complex. It only needs to create a discriminable signal perceivable at a reasonable distance that reliably indicates a single quantity. If reliability were not an issue, such signals could be extremely simple and extremely cheap. Most of a fitness indicator's complexity arises from the reliability requirement. The peacock's tail is complex not because it has to transmit a lot of information, but because it has to work very hard to show that its information is credible. Sometimes, the reliability of fitness indicators is guaranteed by their raw physical size: unfit individuals cannot spare the matter and energy to grow such indicators. But often, indicators evolve to indicate fitness by advertising a component of fitness called developmental stability (Gangestad & Thornhill, 1997; Møller & Swaddle, 1997). This refers to an animal's ability to grow an organ according to a precise design despite perturbations by genetic mutations, environmental damage, and developmental accidents. One convenient way to advertise developmental stability is by growing bilaterally symmetric displays. Perfect symmetry indicates high developmental stability. Random deviations from perfect symmetry, called "fluctuating asymmetry", are markers of lower fitness. Although very subtle asymmetries all over the body can be measured by scientists with calipers, more pronounced asymmetries on sexual ornaments appear to be perceivable by animals choosing mates (Møller & Swaddle, 1997). Developmental stability can also be advertised by other morphological traits: regularly spaced stripes, radially symmetric dots, uniform planes of color, regular patterns of hair growth, even teeth, smooth complexion. Less well understood are the means whereby certain behaviors can advertise the developmental stability of underlying brain structures.

Thus, the pressures to advertise developmental stability may become the principal source of complexity in the fitness indicator. Often, this results in a characteristic pattern of complexity, in which discrete elements are repeated in such a way that another animal may easily notice deviations from regularity. The elements themselves must include enough structural complexity that one can be compared with another. At the behavioral level, this may lead to indicators that incorporate rhythmic elements and repeated motifs, as in the songs and dances of birds and humans. From the viewpoint of signaling theory, repetitions across space (bilateral symmetry, radial symmetry, stripes) and across time (rhythm, repetition) are efficient ways to indicate developmental stability, a major component of fitness. But from the viewpoint of traditional criteria for measuring organic complexity, perfect repetition is comparatively uninteresting, because it can be generated by such simple developmental mechanisms. Here again we have a difference between adaptationist criteria applicabe to fitness indicators versus those applicable to other traits.

Modularity

One of evolutionary psychology's most distinctive ideas is the expectation that human minds are massively modular, composed of hundreds of distinct psychological adaptations that evolved to solve distinct ancestral problems of survival and reproduction. The rationale for massive modularity has been the supposed trade-off between generality and efficiency: "As a rule, when two adaptive problems have solutions that are incompatible or simply different, a single general solution will be inferior to two specialized solutions. In such cases, a jack of all trades is necessarily master of none, because generality can be achieved only by sacrificing effectiveness" (Cosmides & Tooby, 1994, p. 89). Just as there is a different software product available for every distinct computational problem, we expect evolution to have produced a different psychological adaptation for every sufficiently distinct adaptive problem. Modularity is obvious for morphology: animals have distinct limbs, senses, and organs to do different things. Mental modularity has been less obvious to psychologists, but evolutionary considerations of functional efficiency suggest the mind should be at least as modular as the body.

These modularity arguments remain compelling for most types of adaptation. However, fitness indicators raise some problems for modularity. The whole point of fitness indicators is that they should tap into individual differences in general fitness. This typically requires that an indicator have some profound overlap with a wide range of adaptations at some fairly fundamental level. A totally modular indicator that had no functional overlap with other adaptations could not function as a reliable indicator at all. This is because an animal's "fitness" is a statistical abstraction across the efficiency levels of all of the animal's distinct adaptations. Such an abstraction is possible when there are genetic and phenotypic covariances between adaptations (see Houle, 1991). General fitness, considered from a factor-analytic viewpoint, does not exist apart from these covariances between adaptations. To advertise general fitness, then, requires somehow tapping into the efficiency levels of a wide range of functionally distinct adaptations. If an indicator could not work around the selection pressures in favor of functional specialization and modularity, it could not work as an indicator. Total modularity would make indicators totally unreliable. (This does not mean that indicators are "general-purpose devices", whatever that might mean. On the contrary, they may be highly specialized to perform the function of sending signals regarding one's fitness to particular types of receivers under particular conditions).

Typically, indicators work by tapping into lower-level developmental or physiological mechanisms that are expressed in a range of adaptations. We already saw how symmetric sexual ornaments could tap into a fitness component called developmental stability that is manifest in almost all morphological and neurological structures. If some psychological adaptations evolved principally as fitness indicators, we might expect them to tap into fitness components of a more psychological or neurophysiological nature. In particular, we would expect such indicators to capture individual differences in the efficiency of a wide range of psychological adaptations. The adaptations, including the indicators, would be modular at the functional level, but they would overlap considerably at lower levels of implementation, such as elementary cognitive operations or basic neural signaling effects. The overlap would represent what we mean by general fitness, applying to psychological traits.

The resulting cognitive architecture would present two very different faces to psychologists. To those interested in human universals, the mind would look highly modular, with distinct psychological adaptations shaped by survival, social, and sexual selection for different functions. But to those interested in individual differences, the mind would look like a tightly knotted network of inter-correlations. The latter seems to

be a reasonable model of the mind as we know it. Evolutionary psychologists have powerful theoretical and empirical arguments for characterizing the mind as highly modular (Hirschfeld & Gelman, 1994). Yet psychometricians ever since Spearman in 1904 have collected a vast amount of data showing that individual differences in the functional efficiencies of different mental abilities are often highly inter-correlated (Jensen, 1998). When the functional inter-correlations are subject to any reasonable method of factor analysis, a "*g* factor" or "general intelligence" factor always emerges. From the viewpoint of sexual selection theory, this *g* factor simply reflects the psychological and neurological components of general biological fitness, and the mental traits that we praise as indicating high intelligence are simply fitness indicators that evolved through social and sexual selection to display that *g* factor. This may resolve the apparent conflict between of massive modularity at the level of psychological adaptations and massive inter-correlations in functional efficiency at the level of individual differences.

The variance criteria
        The next three criteria (low phenotypic variance, genotypic variance, and heritability) depend on a theoretical argument dating to R. A. Fisher (1930). The argument goes as follows. The reason for expecting low variance in adaptations is the optimizing power of selection. Selection always maximizes fitness, by definition. But every particular trait has costs. These costs imply that for almost every trait, there will be an intermediate optimum at which fitness benefits are maximized relative to fitness costs. (This is obvious to engineers: in a world of limited resources, the best we can do is to optimize designs given the costs of components.) Thus, at evolutionary equilibrium (i.e. for most traits, most of the time, in most species), each trait will be subject to stabilizing (variance-reducing) selection that favors this optimum design. If selection is reasonably strong relative to mutation, the species should converge on this optimum fairly quickly. At the genetic level, this convergence usually implies the elimination of most polymorphisms at loci relevant to the trait, and fixation on just one optimal set of alleles.
        Thus, stabilizing selection should tend to eliminate genetic variation underlying the trait. Without any genetic variation in the trait, heritability should not be higher than zero (see Charlesworth, 1987). Moreover, stabilizing selection should tend to make the trait's expression resistant to environmental perturbations. The trait's development should become strongly canalized. This should lead to low levels of phenotypic variation as well (see Bull, 1987). In summary, every adaptive trait should have an intermediate optimum, and at evolutionary equilibrium, stabilizing selection should minimize genotypic and phenotypic variance in all such traits.
        This standard evolutionary genetics view predicts low phenotypic and genotypic variance and low heritability in all adaptations that are under reasonably strong selection. When we see human traits that show dramatic individual differences in ability and high heritability, these criteria would lead us to doubt their adaptive significance. This creates problems for evolutionary psychology because almost every human mental trait ever assessed shows at least moderate heritability (Bailey, 1998; Plomin, Defries, McClearn, & Rutter, 1997), and heritabilities can be quite high for traits such as intelligence and language ability that were presumably strongly selected in our lineage (Miller & Todd, 1998). Such data suggest that the theoretical argument for low variance in adaptations must be wrong. But how is it wrong?
        A major problem is the existence of mutation. Biologists have realized that mutation is a strongly corrosive force in evolution (Kondrashov, 1988; Pomiankowski & Møller, 1995; Rice, 1988; Rowe & Houle, 1996). Over the last twenty years, it has

turned out to be much more significant than expected, undermining the minimum-variance arguments derived from optimality arguments in population genetics. The new mutationist view suggests that every trait is subject to a balance of forces between mutation and selection. Mildly harmful mutations are constantly arising in the DNA sequences of the many genes (quantitative trait loci) that underlie complex traits. Almost all mutations impair functioning more than they help it, so mutation is generally "negatively biased", reducing each adaptation's efficiency below optimum.

For ordinary traits, mutation's ubiquity does not matter a great deal. Stabilizing selection presumably still operates on such traits to minimize genotypic and phenotypic variation. We simply expect low variance in adaptations rather than zero adaptations. Most importantly, we still expect lower variance in adaptations than in non-adaptations, which are not subject to such strong stabilizing selection.

However, for traits that function as fitness indicators, mutation forces us to step through the looking glass into a wonderland of counter-intuitive effects. If mildly harmful mutations are ubiquitous, then we expect fitness itself to remain genetically heritable most of the time, in most species (Kondrashov, 1988; Rice, 1988). If fitness is usually heritable, then fitness is usually worth advertising with fitness indicators, especially to potential sexual partners. And if fitness is usually heritable, those potential sexual partners will have good reasons to pay attention to fitness indicators, because the mutation load of their offspring will depend on their mate choice decisions. As several biologists have realized, this can lead to situations where fitness indicators amass higher, not lower levels of genotypic and phenotypic variance (Pomiankowski & Møller, 1995; Rowe & Houle, 1996).

Especially relevant here is the "genic capture" model developed by Locke Rowe and David Houle (1996). They proposed that fitness indicators should be favored that capture the greatest proportion of an animal's total fitness in the manifest display. Fitness indicators should evolve higher fitness-dependence and fitness-sensitivity. One way for indicators to do this is to evolve extreme sensitivity to an animal's energy budget, so animals with high-energy reserves can afford a very impressive indicator, while those with low energy reserves may not display the indicator at all. Another way to increase fitness-sensitivity is for an indicator to recruit a large number of genes in its development. The larger the number of genes, the better the indicator gets at revealing overall mutation load across genes. (Heritable fitness can be interpreted as total mutation load, to a first approximation.) Genic capture refers to this postulated evolutionary process whereby fitness indicators come to depend upon, and hence represent the mutation load of, a larger and larger number of genes. Extremely useful indicators would represent a large "mutational target size": they could be disrupted by harmful mutations at a very large number of loci. (Since about half the human genome appears to be expressed in the human brain, the mutational target size of the brain is enormous. This may be why human psychological adaptations make such good fitness indicators.)

The genic capture model predicts that fitness indicators should evolve high genetic variance and high phenotypic variance. These can be measured with coefficients of variation (dimensionless measures that result from dividing the standard deviation in a metric trait by the mean of the trait). Møller and Pomiankowski (1993) found that in barn swallows, tails have higher coefficients of variation than wings, because tails are sexually selected as fitness indicators while wings are subject to stabilizing survival selection. Coefficients of variation are only meaningful for metric traits that can be measured on a ratio scale with a true zero point. Evolutionary psychologists should make it a high priority to develop ratio measures of human mental traits (if such a thing is possible), so we can compare coefficients of variation across

traits and across species. (IQ and personality trait measures are not true ratio scales, but some physiological correlates of mental traits could be measured on a ratio scale).

The prediction about heritability is less clear. If a trait evolves to indicate an animal's current "condition" (e.g. energy reserves, parasite load), and if that condition depends more on the local environment than on the animal's genotype, then the trait may show low heritability. But if a trait evolves principally to indicate heritable fitness (e.g. mutation load), then the trait should show very high heritability. Unfortunately, it is much easier to measure heritability for human mental traits (which are not very informative about adaptive function) than to measure their coefficients of variation (which are). In any case, the standard argument that adaptations should show low variance and low heritability is clearly wrong for fitness indicators.

The universality criteria

During most of the 20th century, the human sciences used the most conservative and uninformative criteria for identifying human mental adaptations: the universality criteria. According to the standard social science model (Tooby & Cosmides, 1992) widely accepted in anthropology and psychology, genetically evolved aspects of human nature should appear uniformly across all historical epochs, all cultures, and all normal humans. Anything else must be attributed to learning, culture, or socialization.

These universality criteria excluded from human nature any psychological adaptations that evolved to show specific effects according to age or sex, or that evolved some strategic sensitivity to local social conditions, local mating systems, demographics, or ecological environments. This left very little human psychology in the category of adaptation. Worse, "evolved" became confused with "innate", so any adaptation that was not fully functioning at birth was considered a result of environmental learning or conditioning. Moreover, cultural anthropologists attained academic status largely by trading in behavioral exotica, presenting different cultures in the most alien light possible, and minimizing commonalities. Despite these hurdles, some anthropologists managed to identify a number of human universals (Brown, 1991).

Evolutionary psychologists are somewhat ambivalent about universality criteria (see Pinker, 1997). When a measurable behavioral pattern, facial expression, verbally expressed emotion, or pattern of childhood development appears to be genuinely universal across time and culture, we are happy to cite that universality as evidence for an underlying psychological adaptation. But when overt behavior varies, we seek universality at the more abstract level of a postulated psychological adaptation that is sensitive to biologically significant environmental variables (e.g. Buss, 1989; Daly & Wilson, 1988; Pinker, 1997; Tooby & Cosmides, 1992). This strategy of looking for universals at a variety of levels of description has allowed evolutionary psychology to claim a larger share of the human mind for the adaptationist program.

However, universality criteria are very tricky to apply to behavioral adaptations that evolved as fitness indicators. One reason is that fitness indicators evolve to amplify apparent individual differences in fitness. That is their principal function. If they presented a uniformity of signals within the species, they would be useless for discriminating between individuals. Universality would undermine discriminability. Therefore, we expect fitness indicators to show the opposite of universality with respect to signal quantity and quality.

Also, behavioral fitness indicators such as bird song are subject to strategic control by an animal's nervous system. Animals can make cost-benefit assessments of when it is worth producing the fitness-indicating behavior. Because these behaviors are costly by design (so they work as strategic handicaps), but bring high potential reproductive rewards, many animals may find themselves balanced on a cost-benefit

knife-edge. Small changes in environmental factors such as food availability or population density may produce large changes in the frequency of a fitness-indicating behavior. Also, because individuals will differ in fitness, placing them at different points on the cost-benefit curve, there will be large individual variations in the amount of behavior produced. The strategic sensitivity of fitness indicators, coupled with their high costs and high potential benefits, may often lead to large individual differences in the quantity and quality of behavioral output. For fitness indicators, we should not expect a stable, universal pattern of behavioral output.

In the case of humans, strategic sensitivity adds a third difficulty. We appear to have evolved a number of behavioral fitness indicators that operate through different display channels: art, music, dance, sports, religious ritual, conspicuous consumption, and so forth. Suppose individuals can assess their relative strengths and weakness in different display domains, and focus their energies on the domain in which they are most likely to excel. We may all be capable of rudimentary display behaviors in every domain, but we may specialize during adolescence and young adulthood. Especially when sexual competition resembles a winner-take-all contest, there are strong pressures to specialize; so one has a reasonable chance of winning high status for one class of display behaviors, even if one is below average in all other classes. This can lead to each individual avoiding all display domains other than their favorite, in order to create a positive impression and avoid embarrassment. The result can be a pattern of behavioral variation across individuals that looks like a diverse set of learned skills. Yet each "skill" may depend on a psychological adaptation that evolved as a fitness indicator. Different cultures may also privilege certain classes of display behavior over other classes, leading to great diversity across time and cultures in the allocation of effort between different fitness indicators.

To survive, one must do many things reasonably well. To advertise one's fitness though, it is sufficient to do one thing extremely well. Animals usually resemble each other quite closely in their survival behaviors, but diverge dramatically from each other in their display behaviors. This display divergence occurs between species, between cultures, and between individuals. Display divergence undermines the usefulness of universality criteria for identifying human psychological adaptations that evolved as fitness indicators.

Conclusion

The identification of psychological adaptations is the heart of evolutionary psychology. Reasonable criteria have been developed for identifying adaptations that evolved to fulfill many survival and social functions. However, these criteria are not very applicable to adaptations that evolved as fitness indicators to deter predators, intimidate rivals, or attract mates. If evolutionary psychology does not expand its view of adaptation, these fitness indicators will continue to be overlooked. Since these fitness indicators are likely to encompass exactly those mental traits that show the highest individual differences and the most dramatic display behaviors, analysis of these indicators may have the most immediate relevance to applied areas such as education, economics, clinical psychology, and human mate choice. The development of new and better criteria for identifying psychological adaptations, including fitness indicators, should be a major step in evolutionary psychology's methodological maturation over the coming years.

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